

CLINES, CONVERGENCE AND CHARACTER DISPLACEMENT IN NEW CALEDONIAN DIPLOMMATINIDS (LAND PROSOBRANCHS)

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ABSTRACT

Eleven diplommatinid species, seven of them previously undescribed, are found in New Caledonia and adjacent islands. Two species are endemic to the adjacent islands, and the nine New Caledonian mainland species show varying degrees of endemism. Up to three species were found to be sympatric. These diplommatinids occur from 0 to 1000 m in elevation, in very dry to very wet environments. All the species live in more or less decomposed leaf litter.

Species vary considerably in both shell size and shape, and form a continuum of shell characters. In many cases the species can be distinguished only by their anatomy. Except in cases of species interaction, shell shape is correlated with moisture. Species exhibit clinal variation in shell characters that are related to environmental conditions. Shell characters overlap when species are allopatric, and diverge when sympatric. This type of character displacement is so common that the clinal variation could be interpreted to be the result of species interaction on a large scale.

The female genital apparatus exhibits four evolutionary steps in a process which may be either the acquisition or the loss of a seminal receptacle. This process probably occurred many times in the diplommatinid stock. Added to this the probable convergence of shell characters makes the value of supraspecific names dubious.

INTRODUCTION

The original purpose of this study was to discriminate among and accurately describe the New Caledonian species of the family Diplommatinidae, which were poorly known from only a few samples of shells collected at the end of the last century. Sorting out the species of these very small land proso-branchs, one to four millimeters high, was in fact very difficult. It is always easy to distinguish several species when they occur together and in a small number of samples. However, the more than one thousand shells collected in fifty-six New Caledonian localities form nearly a continuum in shell characters. It became obvious that the shell characters used for discriminating species since Kobelt's revision (1902) are inadequate to describe species and supraspecific groups. This study attempts only to address the problems at the specific level. The problems at the generic and suprageneric level, in particular the definition of genera and the history of the group from a biogeographical point of view, cannot be solved without much more data. Accordingly, supraspecific levels will be treated only superficially.

This study is based on two main ideas: 1)

the female genital anatomy is less variable than other characters, and allows one to recognize to which species an animal belongs; all other characters can be convergent; 2) Peake's observation (1973) that sympatric species do not overlap morphologically proved particularly useful and stimulated my search for character displacement and analyses of clines.

Diplommatinid distribution and nomenclature

Since Tielecke (1940) established his classification of the superfamily Cyclophoracea, the family Diplommatinidae (= Tielecke's Cochlostomatidae: Solem, 1959) is divided into two subfamilies: the Cochlostomatinae of Europe and the Diplommatininae, which are mainly east Asian and possibly include the doubtfully attributed South American *Adelopoma*. In the western Pacific region, the Diplommatininae occur in Japan, the Marianas, Caroline, Palau, Bismarck, Solomon, Fiji, Samoa and Tonga islands, and reach Norfolk and Lord Howe islands and eastern Australia (Solem, 1959: fig. 17). Most genera are relatively well defined on the basis of their shell characters, but this is not the case in the *Diplommatina-Palaina* group to which all the

southern species belong, including the New Caledonian ones. Rensch (1929) and Van Benthem Jutting (1948) considered that the presence of an apertural tooth characterizes *Diplommatina*, but the study of some Solomon Island species (Solem, 1960b; Tillier, unpublished) and of New Caledonian species (this study) shows the insignificance of this character in taxonomy, even at the specific level. Although Peake (1973) relegated Solomon islands species to *Diplommatina*, *Palaina* is used here for New Caledonian species (as was done by Solem (1959) for New Hebridean ones) for the sole reason that the type-species of *Palaina* is found to be geographically much closer to New Caledonia than the type-species of *Diplommatina*. This choice is arbitrary and does not allow any conclusions about relationships within the group. At least *Palaina macgillivrayi*, which is the type-species from Lord Howe Island, does not seem incompatible in any character with New Caledonian species with reference to the generic level (Figs. 1, 2).

Kobelt & Moellendorff (1898) and Iredale (1937, 1944, 1945) used shell shape as a supraspecific character within *Palaina* (names listed by Solem, 1959). This study shows that this character cannot be considered diagnostic before all data concerning the variability of the species have been compiled. As comprehensive data are not available for most species, no subgeneric groupings are used here.

Habitat and dispersal

All New Caledonian species are in the leaf mould during the day. They are almost always found at ground level. In only one of the fifty-six collecting localities were they found in humus accumulated at the bases of *Pandanus* leaves. The wetter the environment is, the more they are dispersed in the litter. When the environment dries they tend to concentrate where humus retains moisture, i.e., in decaying wood interstices or in a very small wetter surface of the litter. This pattern probably explains why the most important samples here studied were collected in relatively dry conditions. This need for wet humus may explain why the snails are mostly found in forest, but occasionally they are found in maquis, particularly in the northernmost part of New Caledonia, where the latter provides sufficient plant cover. When several species are found together, field observations do not show any

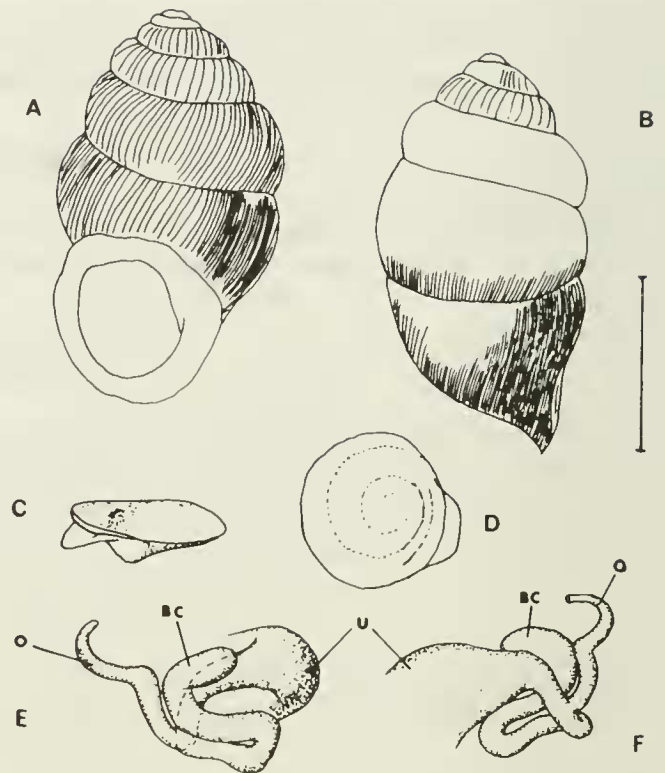


FIG. 1. *Palaina macgillivrayi*, Mt. Gower, Lord Howe Island, 820 m, AMS-C 191369. A and B, shell; C and D, operculum; E and F, female genitalia. Scale line, A and B, 2.5 mm, C, D, E and F, 1.25 mm. BC, bursa copulatrix; O, oviduct; U, uterus.

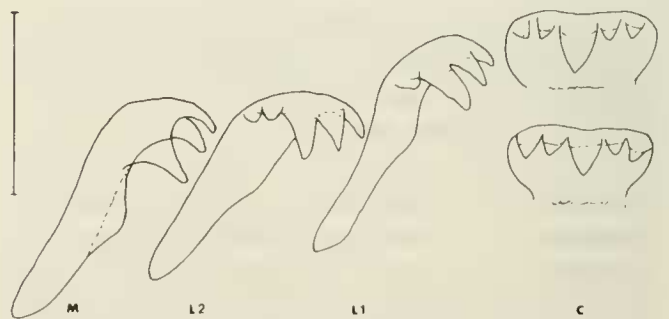


FIG. 2. Radula of *Palaina macgillivrayi*, same animal as Fig. 1. Scale line 0.025 mm.

kind of specialization. Although no accurate test was made, it seems that sampling in a very small surface ($\pm 400 \text{ cm}^2$) in a wet environment gives the same proportions of species as sampling in a larger surface (i.e., a few square meters). In fact, ecological differences among species have been detected only by statistical analyses of environmental variables at each station.

Data concerning the collecting stations are given in Table 1 and Fig. 7. One sees that *Palaina* was not collected in Ouvéa and Lifou. It is possible that we failed to collect them, but it is also possible that *Palaina* has not yet col-

onized them; these two islands are the most recent in the New Caledonian archipelago. On the mainland no *Palaina* was collected higher than 1000 m, and we have collected enough at such altitudes to interpret the absence of *Palaina* as significant. The high altitude stations are wetter and colder than those supporting *Palaina*, but it may also be remarked that in New Caledonian high altitude rainforest, vegetation decays much more slowly than elsewhere. As a result there is an absence of real humus which could be a limiting factor for *Palaina*.

Peake (1968, 1969, 1973) postulated that passive transport was the most important factor in the dispersal of small land snails such as diplommatinids, even within terrestrial areas. If it is true that no other type of transport can be postulated for the colonization of isolated islands such as the Loyalty Islands, this is not the case for colonization inside the mainland of New Caledonia and possibly for the closest islands (Belep Islands, Isle of Pines) which were probably not permanently isolated by the sea. As a matter of fact, the occurrence of clines over small distances is an argument for the predominance of active dispersal. For example, in cases where we observe a cline along a steep slope over a short distance (e.g., *Palaina boucheti* in the Paéoua), the predominance of passive transport down the slope would imply that the variability observed at the summit influences the variability at the bottom. This is not the case in any such cline that we have observed; on the contrary, the few aberrations observed (e.g., *Palaina mariei* on the Paéoua) consist in the presence of the low altitude form also at the summit. This suggests that the dispersal is active, and we have no reason to presume that *Palaina* spreads inside each island by other major means (small mammals are absent and birds scarce).

Radula and feeding

I have not found any specific differences between New Caledonian *Palaina* radulae. All are taenioglossate with similar teeth (Fig. 3). The central tooth has generally five cusps, the first lateral four, the second lateral three or four, and the marginal teeth have two or three; the minor variations in number of cusps are caused by their partial or total fusion. As indicated by Peake (1973), the *Palaina* species are probably grazers. It is quite surprising to observe that the size of the teeth and their

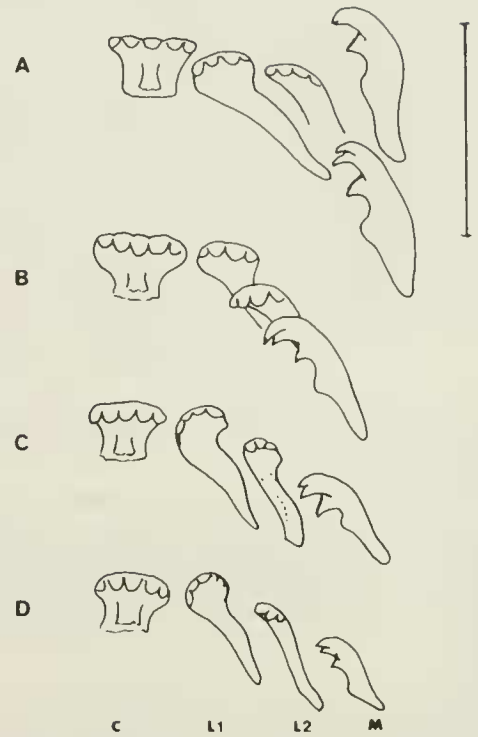


FIG. 3. Radulae of New Caledonian *Palaina*. A, *P. montrouzieri*, Lindéralique (sta. 11). B, *P. perroquini*, Mt. Guemba (sta. 47). C, *P. mariei*, Mé Maoya (sta. 28). D, *P. nanodes*, Touaourou (sta. 48). Scale line 0.025 mm.

cusps vary much less than the size of the animals (Fig. 3). The central tooth is always about the same size in all species and the greatest differences in size are found in the marginal teeth. However, the size of the latter varies only in the ratio 1:2 as the shell height varies in the ratio 1:4. When compared with the very large differences in the size of the animals, this radula similarity suggests that animal size is not related with food as suggested by Peake (1973). The niches of the sympatric species are therefore probably not differentiated by the particle size of the food, for which competition possibly occurs.

Shell and operculum

All New Caledonian, Australian and some of the Solomon Islands species of *Palaina* have similar opercula. They are thin, corneous, slightly concave and oligogyrous (Fig. 4; Tillier, unpublished). The opercula of these species have an arcuate, narrow thickening, parallel to the columellar border; they are attached to the foot by their central area, which is granulous. In some Solomon Islands and Lord Howe Island species, the operculum is more developed and is fixed to the foot by a lamellar process, protruding internally, and

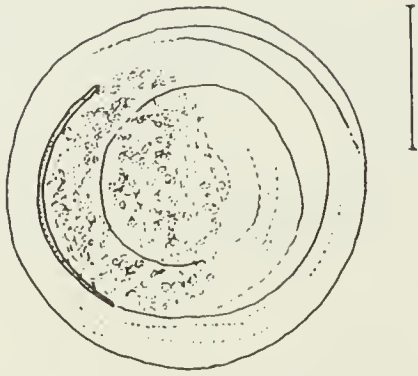


FIG. 4. Operculum of *P. mariei*, Mé Maoya (sta. 28). Scale line 0.125 mm.

parallel to the columellar side of the aperture (Fig. 1c, d). The thickening of New Caledonian opercula is probably homologous to this process.

Shell shape varies from a high and conical morphotype, called *Macropalaina* as a genus by Moellendorff (1897), to a short and stout one which may be called *Palaina*, or even *Cylindropalaina* when the shell approaches a perfect cylinder in shape. All intermediates occur and could be called the *Velepaina* morphotype. Each species has a definite range of morphotype variability, either from *Macropalaina* to *Velepaina* and *Palaina* or from *Velepaina* to *Palaina* and *Cylindropalaina*. None of these names can have taxonomic value until each type-species has proved to represent a distinct group of species within the *Diplommatina-Palaina* complex. It will be demonstrated further that the variations of the morphotypes are correlated with environmental conditions, and in particular with moisture. Comparisons with morphotypes found in other Melanesian regions may be interesting. The *Velepaina* morphotype is found in eastern Australia and in the New Hebrides (Iredale, 1937; Solem, 1959). In Australia, *Eclogarinia* represents a morphotype characterized by a high conical shell with the penultimate whorl narrower in diameter than the preceding one. "*Eclogarinia*" *gowl-landi* does not exhibit any other peculiar anatomical or morphological feature (Tillier, unpublished). This morphotype is quite common farther north and is found also in New Guinea. In the Solomon Islands shell shapes vary between this type and typical *Palaina*, with intermediates quite similar to the stoutest shells of the New Caledonian *Palaina perroquini* (Fig. 29A; Peake, 1973, Fig. 1). Lord Howe Island species vary around the typical *Palaina* morphotype (the type-species among them!),

whereas the two Norfolk Island species have a loose last whorl but otherwise approach the *Velepaina* morphotype (Iredale, 1945). Sinistral species are dominant in Australia and the Solomon Islands, and no dextral species is found in New Caledonia, New Hebrides, Norfolk and Lord Howe Islands.

All New Caledonian species have thin shells, with an ornamentation consisting of very thin spiral threads crossed by radial lamellae, which may project as wings in well-preserved juvenile specimens of some species. The distances between ornamental elements on each whorl vary but tend to be different in each species. In well-preserved specimens it can be observed that the spiral threads are continuous over the radial lamellae. Just before the adult aperture is formed there is no significant change in the interval between successive radial ribs. A first peristome is formed by the expansion of one rib, and then the ribs are very close and not expanded on a very short distance before the definitive expanded peristome is formed (Fig. 26). In all species but one, the peristome is approximately parallel to the shell axis.

This type of ornamentation and aperture is the commonest in Melanesia, but all Solomon Islands species and some Lord Howe Island species have a thicker shell and a different type of aperture. In these species, the radial ribs become closer about one quarter of a whorl before the peristome is formed; the latter is very thick and formed by crowded, slightly expanded radial ribs (see Rensch, 1929, fig. 6 and *Palaina macgillivrayi*, Fig. 1b).

The embryonic shell is irregularly pitted in the same way in all New Caledonian species, and is similar in other Melanesian species examined.

Animal and general anatomy

A preserved animal is shown in Fig. 5. The most striking feature is the well-defined propodium, mesopodium and metapodium, which are separated by distinct and constant grooves. This feature, which is exceptional in marine mesogastropods (Fretter & Graham, 1962), may also be seen in the Cochlostomatinae. According to Girardi's figures (1978), such grooves are absent in poteriids. This character could serve to define families, but unfortunately I could not check it in other Cyclophoracea and cannot reach any definitive conclusion. Among other land proso-

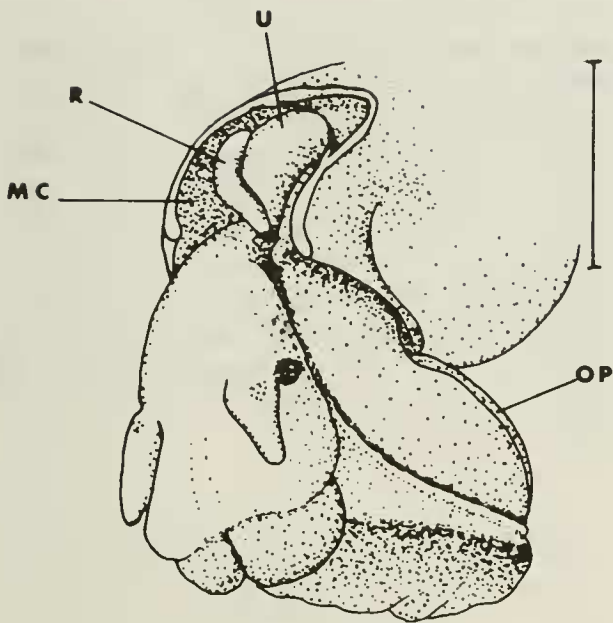


FIG. 5. Animal of *P. montrouzieri*, Pombei (sta. 13). Scale line 0.5 mm. MC, mantle cavity; OP, operculum; R, rectum; U, uterus.

branches, pedal grooves are found also in truncatellids (Fretter & Graham, 1978).

The mouth opens into a slit between two well-defined, rounded lobes. Above these lobes the head forms a sort of apron, posteriorly limited by the anterior pedal groove which separates the propodium from the mesopodium. The animals are completely white, except the tentacles that are sometimes grey. There is always a grey spot at the base of the tentacles, in front of the eyes. This spot may be either rounded (Fig. 5) or form a transverse bar joining the eye; its shape is neither specific nor sex-determined, although each individual shows one or the other of the two spot shapes.

The mantle cavity occupies about the last one and a half whorls of the visceral mass (Fig. 6). The uterus or prostate runs along the columellar side of the mantle cavity, without protruding into the upper visceral cavity, and is bordered externally by the rectum. The kidney occupies about one quarter of a whorl above the upper part of the mantle cavity and hides the small heart that lies just under its proximate extremity. The oesophagus runs up along the columella before bending back outwards into a large cylindrical stomach, about one third of a whorl long. The stomach has no distal caecum but a distal inflated ring, which is probably the equivalent, whereas the Cochlostomatinae have a true caecum. Fecal pellets are formed in the proximal intestine which is parallel to the spire, less than half a

whorl long and often regularly inflated by fecal matter. In the distal intestine the pellets are always well formed and distinct. Just proximally to the mantle cavity, the intestine forms one loop before running into the latter between the pallial gonoduct and the kidney. The same disposition is found in the Cochlostomatinae. Among Cyclophoracea poterids have the same type of stomach but without any trace of a caecum (Girardi, *in litt.*; data lacking for other families).

Genital anatomy, reproduction and growth

Males have no penis, and thus males and females have the same disposition of their genital apparatus. The gonad lies along the columellar side of the visceral mass for about one whorl, starting from the beginning of the third whorl from the apex. The genital duct then coils along the columella, together with the oesophagus, to the upper parietal corner of the mantle cavity aperture where it opens just beside the anus (Figs. 5, 6). At the proximal end of the mantle cavity it enlarges

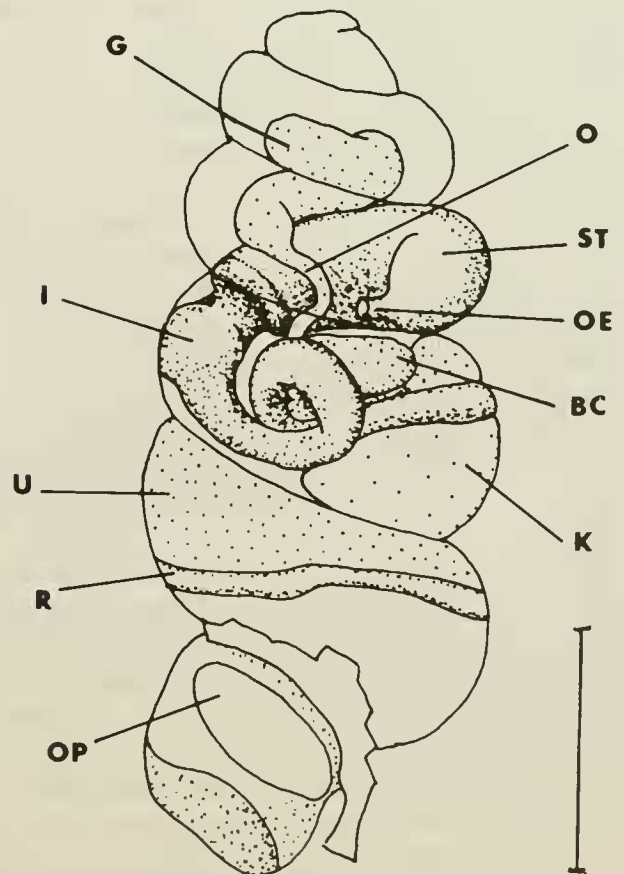


FIG. 6. General anatomy of *P. mariei*, Mé Maoya (sta. 28). Scale line 0.5 mm. The upper intestine is inflated by a pellet. BC, bursa copulatrix; G, gonad; I, intestine; K, kidney; O, oviduct; OE, oesophagus (sectioned); OP, operculum; R, rectum; ST, stomach; U, uterus.

abruptly into a prostate or a uterus. In males there is no other morphological differentiation, but in females the differentiation of the distal oviduct, just proximally to the upper extremity of the uterus, into a bursa copulatrix and a seminal receptacle provides the only specific anatomical characters that I could find in *Palaina*. These female organs are located behind the intestinal loop (Fig. 6).

The bursa copulatrix is relatively constant in shape and disposition within each species. Its inflated head is generally appressed against the proximal end of the uterus, but its stalk may point either upwards or downwards from the distal oviduct; in the latter case its head may occasionally, but constantly within a population, point within the intestinal loop instead of above it.

The seminal receptacle may be absent or present, as in the Cochlostomatinae (Giusti, 1971). Four steps in its position and development are found: 1) The seminal receptacle is well developed and opens into the oviduct close to the base of the stalk of the bursa copulatrix: found in New Caledonian *Palaina montrouzieri* (Fig. 20); 2) The seminal receptacle is well developed, but opens into the basis of the bursa stalk: found in some Solomon Islands species (Tillier, unpublished); 3) The seminal receptacle is reduced to a swelling located approximately in the middle of the bursa stalk, on the outside of the bend of the latter: found in New Caledonian *Palaina mariei* (Fig. 22), *P. obesa* (Fig. 23), and in some Solomon Island species (Tillier, unpublished); 4) The seminal receptacle is absent in New Caledonian *Palaina mareana* (Fig. 34), *P. perroquini*, *P. boucheti* (Fig. 25), *P. opaoana* (Fig. 32) and *P. nanodes* (Fig. 27), and in some Australian, Solomon Islands (Tillier, unpublished) and Lord Howe species (Fig. 1).

Only the two extreme arrangements are known in the Cochlostomatinae (Giusti, 1971), and an arrangement somewhat equivalent to the intermediate ones is found in the Pupinidae (Tiecke, 1940) where it is therefore not a familial character.

We have no data on reproductive behaviour, and do not know how individuals recognize each other, the males having no penis. The populations collected are formed of sets of specimens of the same apparent age, and it therefore seems that all individuals of one population reproduce at the same time.

Berry (1963a, b) observed that the space between two radial ribs represents one day's

growth in Malayan *Opisthostoma*. As far as this result can be generalized for any Diplomatinae, this means that species with distant varices grow faster than species with close varices. If this hypothesis is true, the time necessary before New Caledonian species begin to build their peristome varies from about 80 days in *Palaina mareana* to about 160 days in *P. nissidiophila*. The genital apparatus is formed at about the same time as the first expansion of the peristome, but reaches its full development only when the second expansion is built.

SPECIES VARIATIONS AND INTERACTIONS

Schindel & Gould (1977) reviewed and discussed character displacement, with particular reference to land snails. The methodology herein adopted for demonstrating character displacement is very simple, and consists of: 1) An analysis of the relationships between the variations of the species and the variations of their environment; 2) An analysis of the variations found in populations of sympatric species, with reference to the first analysis. I cannot but hope that these analyses provide a rebuttal to Schindel & Gould's statement according to which the fossil record is superior to the living one for assessing such evolutionary processes.

Materials and methods

More than 1000 specimens, collected at 56 stations all over New Caledonia and adjacent islands, were used for this study. Shells are much more numerous than animals taken alive, but living animals were found at 33 stations. Two samples were borrowed from the National Museum of New Zealand (NMNZ), Wellington; all the other specimens are housed in the Muséum national d'Histoire naturelle, Paris (MNHN), and consist of: 1) A few old samples, collected mainly by Marie around Nouméa and the Baie de Prony (= Baie du Sud), which are important because they contain most of the previously described type-specimens; 2) About nine-tenths of all the material was collected by Philippe Bouchet between April 1978 and July 1979, and by Bouchet and Tillier in June–July 1979.

A complete list of the stations is given in Table 1, and their localities are shown in Fig.

7. For each station we know the altitude, the type of vegetation and the rainfall. The latter was estimated from Moniod's data (1966) published by ORSTOM. In some cases the value given by the ORSTOM map is aberrant. For example, the northwestern mountains, the summits of which are covered with high altitude rainforest, are in a very dry zone of the map. In such cases I estimated the rainfall as being the same as in another place with the same vegetation where it has been measured.

The number of specimens at each station will be found in brackets within the list of material of each species in the systematic part of this work. Shell height, H , and shell diameter, D , were measured on 937 shells (in one sample of more than 200 shells, only 128 were measured to avoid a disproportionate influence on the results of the analyses). For measurements, shells were placed under the microscope with the aperture upward and dimensions measured on mm paper placed under the camera lucida; precision was $\pm 10 \mu\text{m}$. H is the largest dimension parallel to the shell axis, D is the diameter of the body whorl, perpendicular to the shell axis, from the outer border of the aperture to the most external opposite point of the body whorl. The number of radial ribs should be useful for cline analyses. It was not used because of the impossibility of obtaining reliable counts without counting all the ribs of one shell, which is impractical with such a large number of small shells.

After shells were measured, most of the preserved specimens were dissected. This was useful for establishing anatomical variability of each species and absolutely necessary for naming the specimens representative of the morphological overlap of two species.

Statistical methods

The statistical analysis was made to try to understand the relations, within different sets of specimens, between the dimensions and shape of the shells, and the environmental variables. The IRIS 80 computer of the Université Pierre et Marie Curie, Paris, was used to perform: 1) The analysis of the distribution of the variables with the HISTO program; 2) The factor analysis of several sets of specimens for several sets of variables with the ANACOR program. Both programs come from the statistical library of the computer and

were published by Jambu & Lebeaux, 1979 (HISTO) and Benzécri, 1980 (ANACOR).

All data were first computed in a single matrix with one row for each specimen, numbered from 1 to 937. In each row the characteristics of each specimen are written in nine columns. These variables are the species, coded by a number between 1 and 11, shell height H , shell diameter D , number of the station between 1 and 56, longitude, latitude and rainfall. Two additional morphometric data, which in fact were more significant than height and diameter, were calculated for each specimen and introduced as columns. These are shell size, approximated by the product $H \times D$, and shell shape, approximated by the ratio H/D . The sets of specimens (all specimens from one locality, or all specimens belonging to one species, etc.) and different sets of variables for these specimens were extracted from this general table for the analyses.

The HISTO program then permitted establishing histograms for each quantitative variable, partitioned into twenty classes of equal amplitude. These histograms do not show any classic distribution (normal, γ , etc.) for any variable, even after simple transformations and even when established species by species and population by population. For this reason I turned to factor analysis (correspondence analysis), which may be used without any preliminary hypothesis about the distribution of the variables. As correspondence analysis requires nearly equal frequencies of the classes, the basic histograms were used previous to each analysis to establish class limits allowing subequal effectives of classes. As a result the same symbols do not represent the same absolute values in the different analyses.

Once the variables have been grouped into modalities of equal effectives, the ANACOR program analyses the matrix coded 0 or 1. It locates each individual in the space of the variables (or each modality in the space of the individuals) and extracts the principal component axes, classified in function of the percentage of variance loading on them. The final result is a projection of the individuals and of the variables on the planes determined by the axes of the principal components. Only the projections of the variables are reproduced here. The projections of the individuals were used to check the verisimilitude of proposed interpretations, but are unreproducible in a printed paper (937 numbered points on each).

TABLE 1. List of collecting stations.

1. Pott (Belep Islands), bay of Panane, thalweg with Gaiacs. Rainfall 1190 mm. Bouchet and Chérel coll. 27.8.1978. 2. Art (Belep Islands), bay of Païromé, littoral dry forest with *Cycas* on sand and pumice. Rainfall 1190 mm. Bouchet and Chérel coll. 25.8.1978. 3. Niénane (Daos du Nord Islands), northeastern bay, littoral dry forest on sand and pumice. Rainfall 1190 mm. Bouchet and Chérel coll. 23.8.1978. 4. Mt. Tiébaghi, 500 m, low maquis on peridotite. Rainfall 1200 mm. Tillier coll. 6.1979. 5. Le Cresson, 100 m, dry forest on calcareous outcrop. Rainfall 1200 mm. Tillier coll. 30.6.1979. 6. Koum, 80 m, dry forest on calcareous outcrop. Rainfall 1200 mm. Tillier coll. 30.6.1979. 7. Mandjélia, 400 m, 5 km from the sawmill, rainforest. Rainfall 1900 mm. Tillier coll. 2.7.1979. 8. Oubatche, 500 m, rainforest. Rainfall 2500 mm. Hedley coll. (AMS). 9. Ruisseau de l'Etoile du Nord (Oué Paoulou), 150 m, dry forest probably on a calcareous outcrop. Rainfall 1100 mm. Tillier coll. 30.6.1979. 10. Kavatche, 50 m, river drift in slightly disturbed rainforest. Rainfall 2200 mm. Bouchet coll. 25.11.1979. 11. Lindéralique, 20 m, decaying plant accumulation in holes in a massive calcareous outcrop. Rainfall 2267 mm. Bouchet coll. 26.11.1978. 12. Taom Mt., 900 m, altitude rainforest in a thalweg, on peridotite. Rainfall 2500 mm. Tillier coll. 3.7.1979. 13. Pombei, 100 m, rainforest. Rainfall 2781 mm. Bouchet and Tillier coll. 7.1979. 14. Momies de la Faténaoué, 150 m, dry forest, Rainfall 1250 mm. Tillier coll. 4.7.1979. 15. Poindimié, 20–50 m, rainforest 300 m from the shore. Rainfall 3200 mm. Bouchet coll. 29.9.1978. 16. Plateau de Tango, track to Bobeitio, 300–350 m, rainforest. Rainfall 1800 mm. Bouchet coll. 24.12.1978. 17. Aoupinié, 350 m, track to the saw-mill above Goa tribe, rainforest. Rainfall 2500 mm. Bouchet coll. 18. Gopin, 50 m, southwestern lower slopes of the Mt. Aoupinié, rainforest. Rainfall 1525 mm. Bouchet coll. 6.5.1979. 19. Forêt Plate, 540 m, slope of Mt. Paéoua, rainforest. Rainfall 1841 mm. Bouchet and Tillier coll. 15.7.1979. 20. Mt. Paéoua, 950–1000 m altitude rainforest. Rainfall 3000 mm. Tillier coll. 5.7.1979. 21. between Nékliai and Nétéa, 100 m, lower slopes of Mt. Boulinda, rainforest. Rainfall 1500 mm. Tillier coll. 7.7.1979. 22. Nindiah, 50 m, near the mission, small calcareous outcrop. Rainfall 1842 mm. Bouchet coll. 30.12.1978. 23. Plaine aux Gaiacs, probably sublittoral dry forest. Rainfall 1000 mm. Dell coll. (NMNZ). 24. Népoui, Presqu'île de Muéo, littoral dry forest. Rainfall 1000 mm. Tillier coll. 5.7.1979. 25. Adio caves, 180 m, decaying plant accumulation in holes in calcareous outcrop. Bouchet coll. 6.5.1979. 26. Col des Roussettes-Bogui, 150 m, rainforest. Rainfall 1600 mm. Bouchet coll. 15.5.1978. 27. Col des Roussettes, 550 m, rainforest. Rainfall 1658 mm. Kuscher coll. 31.10.1978 (NMNZ). 28. Junction of the two rivers running down the Mt. Mé Maoya and the Dent de Poya, 50 m, rainforest. Rainfall 2000 mm. Bouchet and Tillier coll. 15.6.1979. 29. Mt. Mé Ori, 530 m, southeastern slope, rainforest. Rainfall 2000 mm. Bouchet coll. 30.4.1979. 30. Col de Pétchékara-Dothio, 250 m, rainforest. Rainfall 2000 mm. Bouchet coll. 8.7.1978. 31. Oua Oué, 50 m, decaying plant accumulation in holes in calcareous outcrop. Rainfall 1364 mm. Bouchet coll. 31.12.1978. 32. Poé beach, secondary dry forest on sand. Rainfall 1000 mm. Bouchet coll. 19.8.1978. 33. Roche Percée, Bourail, littoral maquis on sand. Rainfall 1000 mm. Bouchet coll. 10.12.1978. 34. Col. des Arabes, 100 m, maquis. Rainfall 1000 mm. Bouchet, Tillier and Warén coll. 9.6.1979. 35. Nassirah, 100 m, on the right slope of the Fonwhary valley, rainforest. Rainfall 1300 mm. Bouchet coll. 8.7.1978. 36. Mine Galliéni, 700–750 m, gallery forest in a thalweg on peridotite. Rainfall 1600 mm. Bouchet coll. 19.5.1979. 37. Mt. Dzumac, 1000 m, altitude rainforest. Rainfall 3000 mm. Bouchet and Tillier coll. 6.1979. 38. Plaine aux Cailloux, 100 m, rainforest. Rainfall 1267 mm. Bouchet coll. 3.2.1979. 39. Ndé, 60 m, hill near the tribe, secondary forest. Rainfall 1267 mm. Bouchet coll. 2.7.1978. 40. Yahoué, 200 m, slopes of the Mt. Koghi, rainforest. Rainfall 1400 mm. Bouchet coll. 24.11.1978. 41. Nouméa, old collections, probably dry forest. Rainfall 1100 mm. 42. Baie Tina, Nouméa, littoral dry forest. Rainfall 1200 mm. Bouchet coll. 16.12.1978. 43. Rivière Bleue, 150 m, rainforest on peridotite. Rainfall 3000 mm. Bouchet coll. 6.1.1979. 44. Mamié, 50 m, high maquis with boulders on peridotite. Rainfall 2800 mm. Bouchet coll. 14.1.1979. 45. Waho, 20 m, rainforest on uplifted coral reef. Rainfall 2800 mm. 46. Mt. Guemba, 200 m, rainforest on peridotite. Rainfall 2938 mm. Bouchet coll. 13.1.1979. 47. Mt. Guemba, 450 m, rainforest on peridotite. Rainfall 3200 mm. Bouchet coll. 16.2.1979. 48. Touaourou, 10 m, rainforest on uplifted coral reef. Rainfall 3000 mm. Bouchet coll. 8.12.1978. 49. Kuébéni, 50–80 m, rainforest on slope on peridotite, left bank of the Kuébéni river. Rainfall 2500 mm. Bouchet coll. 15.2.1979. 50. Goro, 15 m, rainforest on peridotite. Rainfall 1900 mm. Bouchet and Chérel coll. 8.4.1979. 51. Baie de Prony, on peridotite, old collections. Rainfall 2800 mm. 52. Mt. Oungoné, 450 m, rainforest on steep slope. Rainfall 3500 mm. Bouchet coll. 1.10.1978. 53. Ouro, Isle of Pines, 15 m, littoral dry forest on uplifted coral reef. Rainfall 1800 mm. Bouchet coll. 21.10.1978. 54. Enéné, Maré Island, 60 m, wet bottom of a large dolina. Rainfall 1500 mm. Bouchet coll. 7.4.1979. 55. Medu, Maré Island, dry forest on uplifted coral reef. Rainfall 1500 mm. Bouchet coll. 4.1979. 56. Nécé, Maré Island, 15–20 m, dry forest on uplifted coral reef. Rainfall 1500 mm. Bouchet coll. 5.4.1979.

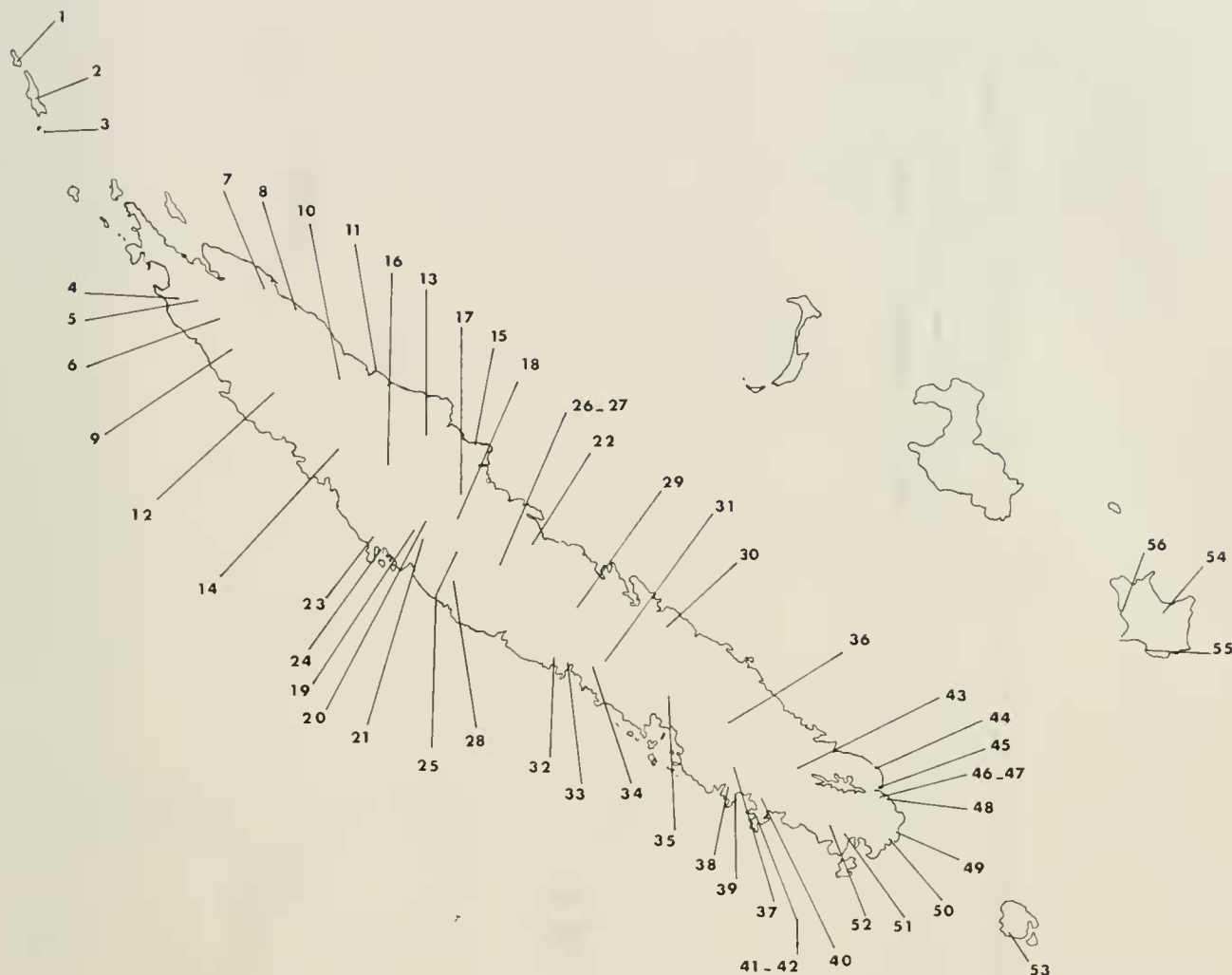


FIG. 7. Map of the collecting localities (listed in Table 1).

Geography, ecology and morphometric variability

Each species exhibits a well defined range for each geographical, ecological and morphometric variable. The specific ranges for height, diameter, size, shape and rainfall are given in Figs. 8 to 11. The geographic data are summarized in Table 2. Altitude was eliminated from this step onwards because its significance, if it has any, is masked by the influence of rainfall; nearly all the eastern coast is very wet from sea level to high altitudes and the rainfall is approximately proportional to the altitude along the western coast. All the intermediate situations are found when crossing New Caledonia.

Palaina mariei is the only species that may be expected anywhere on the mainland, except in the extreme north. It is also the only species that exists in the whole rainfall range

of New Caledonian *Palaina*, from 1000 to 3500 mm a year. It is a rather small species of variable shape, but occupies the mid-range of all shapes. It has been found sympatric with *Palaina montrouzieri*, *P. opaoana* and *P. boucheti*.

Palaina montrouzieri and *P. opaoana* have about the same mid-size, but the former may attain larger sizes than the latter. They are found in the same rainfall range of 1000 to 3125 mm rain a year but occupy adjacent geographic ranges, *P. montrouzieri* being found in northern, central, eastern and possibly southern New Caledonia, and *P. opaoana* being found only in central New Caledonia but very commonly along the western coast. *Palaina montrouzieri* generally has a more elongate shape than *P. opaoana*.

Palaina boucheti is a small species, generally less elongated than *P. mariei*, occurring throughout southern, central, eastern and

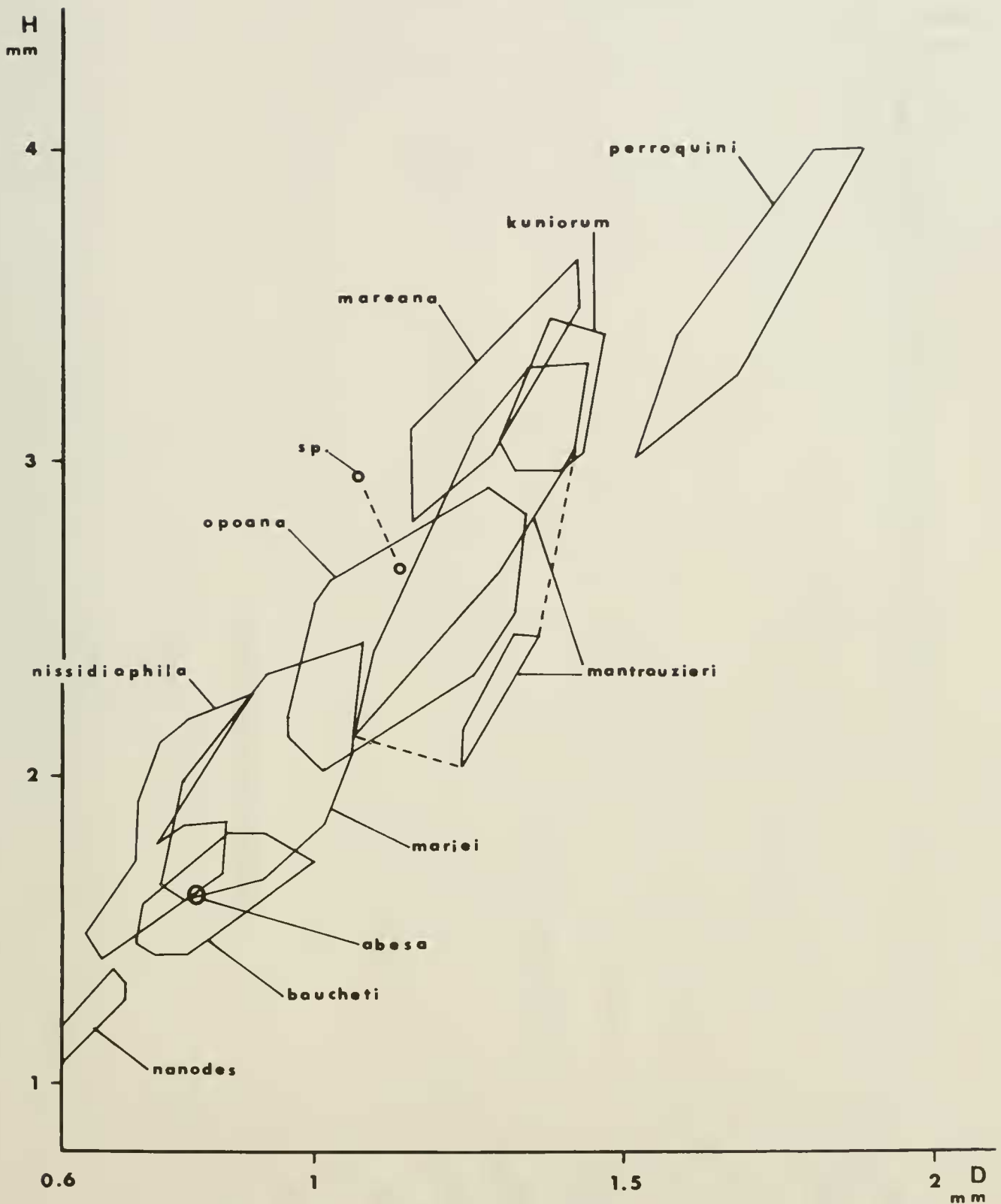


FIG. 8. Scatter diagram of New Caledonian species of *Palaina* for shell height (H) and diameter (D).

northeastern New Caledonia. It was found in areas with rainfall ranging from 1500 to 3500 mm a year.

Palaina nissidiophila occurs only in the Belep Islands and along the northwestern coast of New Caledonia. It attains the smallest sizes found. It is restricted to areas with low rainfall (1125 to 1275 mm rain a year). The species varies enormously in shape.

Palaina perroquini is the largest New Caledonian species. It is restricted to the region south of the great southern mountain mass, with high rainfall (from 2750 to 3125 mm rain a year).

Palaina obesa and *P. nanodes* are both very small and very stout species showing a very restricted endemism in regions with high rainfall, the former in the northeastern moun-

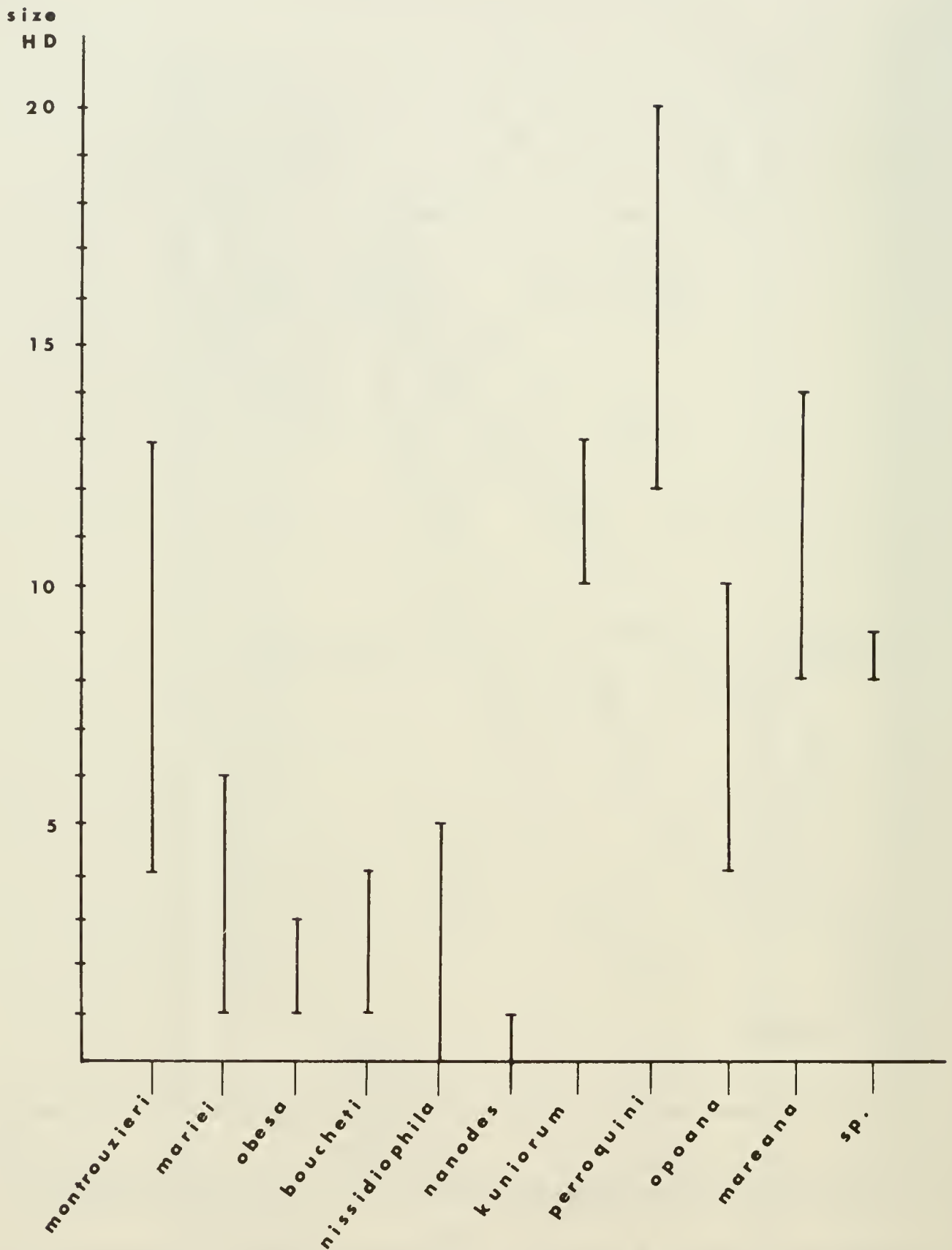


FIG. 9. Size range of New Caledonian species of *Palaina*. Units = total range/20 (= limits of size classes).

tain range and the latter in the southeastern border of the mainland.

Palaina kuniorum and *P. mareana* are both insular endemics, the former in the Isle of Pines (for which Kunié is the Melanesian

name), and the latter in Maré, Loyalty Islands. *Palaina sp.*, seemingly endemic in Adio but known from only two specimens, will be discussed in the systematic section.

Note that species that are most restricted in

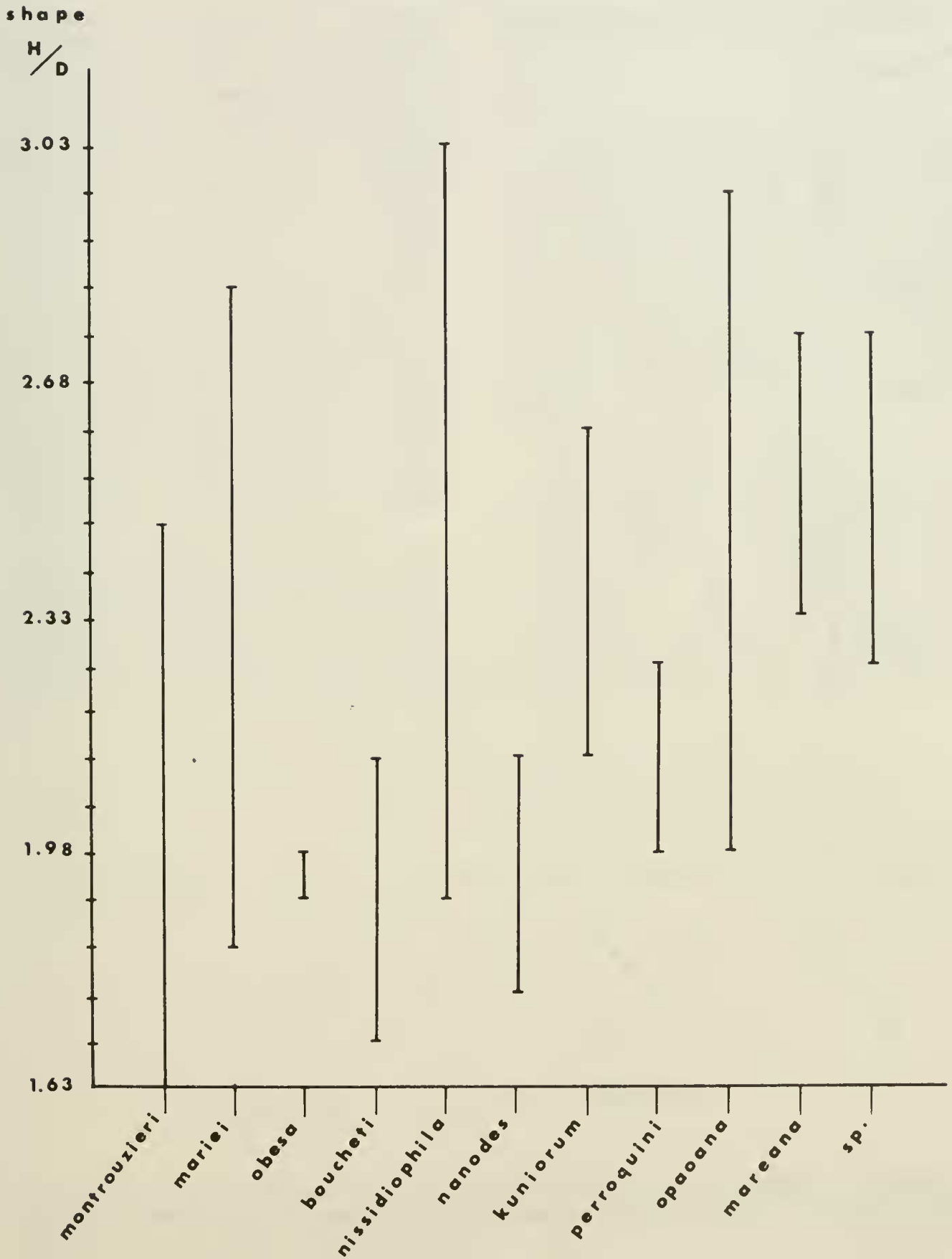


FIG. 10. Shape range of New Caledonian species of *Palaina*.

geographic distribution have a very narrow rainfall range, which was not immediately obvious because of the enormous variation of rainfall over very short distances. Conversely,

Palaina mariei, which is the most widely distributed species, tolerates the widest rainfall range. *Palaina nissidiophila* occupies a relatively wide geographic range although re-

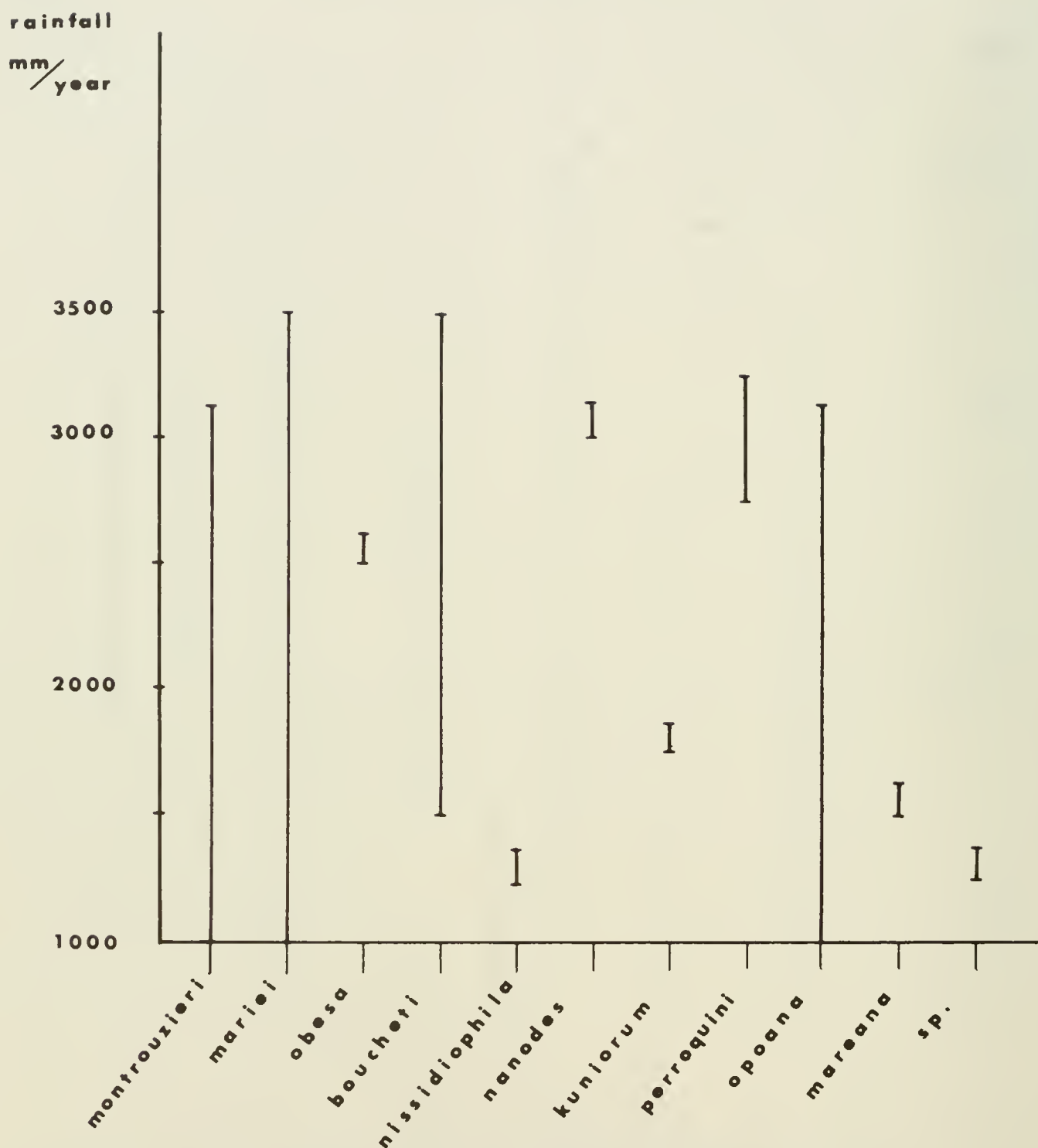


FIG. 11. Rainfall range of New Caledonian species of *Palaina*.

stricted to low rainfall, but is found over the largest homogeneously dry region of New Caledonia.

Rainfall and shell shape

By tracing on Fig. 8 the scatter of each population for H versus D, instead of the scatter of each species, it seems that the lower scatters represent populations collected in high rainfall areas, and that the upper scatters

represent populations collected in low rainfall areas. In other words, it seems that stout shells are found in wetter areas than slender shells (the diagram is not reproduced here because it would be unreadable at a size compatible with printing). To check this, a factor analysis of the contingency table of the variables of shape ($HS = H/D$) and rainfall (PL) was made using the ANACOR program. This table was established with the modalities HS as lines and the modalities PL as col-

umns, and by counting the specimens at each intersection. The class limits corresponding to each modality are given in Tables 3 and 4.

The result of the analysis is shown in Fig. 12. This projection represents 92% of the inertia of the scatter, and the other axes do not change the relative position of the variables. On this projection the axis 2 quite clearly separates low levels of rainfall and elongated shells, on the right side, from very high levels of rainfall and very stout shells well grouped at the extreme left. The complementary projection of the individuals does not show the predominance of any particular species on this result, and thus it may be said that in New Caledonian *Palaina*, the occurrence of very stout shells is linked to very high rainfall, whereas the occurrence of slender shells is linked to low rainfall. Rainfall probably represents the degree of moisture of the environment.

A similar analysis was made for size (HD) and rainfall. It showed a linkage between very high rainfall and extreme sizes, but no general conclusion can be deduced about the selective action of rainfall on size because very large and very small species are not scattered

and appear weighted as species more than as individuals.

Clines

If the scatter of each population is traced on a H versus D diagram, two species exhibit obvious clines for size. The size of *Palaina nissidiophila* increases regularly from the extreme north to the south, between the Belep Islands (sta. 1) and the Faténaoué valley (sta. 14); the shape of the shells is also gradually transformed. The size of *Palaina montrouzieri* also increases from the northwestern Tiébaghi mountain (sta. 4) to the southeastern Lindéralique (sta. 11) through stations 9 and 10.

To understand these clines and to try eventually to discriminate less obvious ones, a factor analysis of the species represented by a large number of specimens over a large area was done. These species are *Palaina montrouzieri* (n = 129 specimens), *P. nissidiophila* (n = 156), *P. mariei* (n = 282), *P. boucheti* (n = 108), and *P. opaoana* (n = 193). The variables analysed were shell shape (HS), shell size (HD), and rainfall (PL).

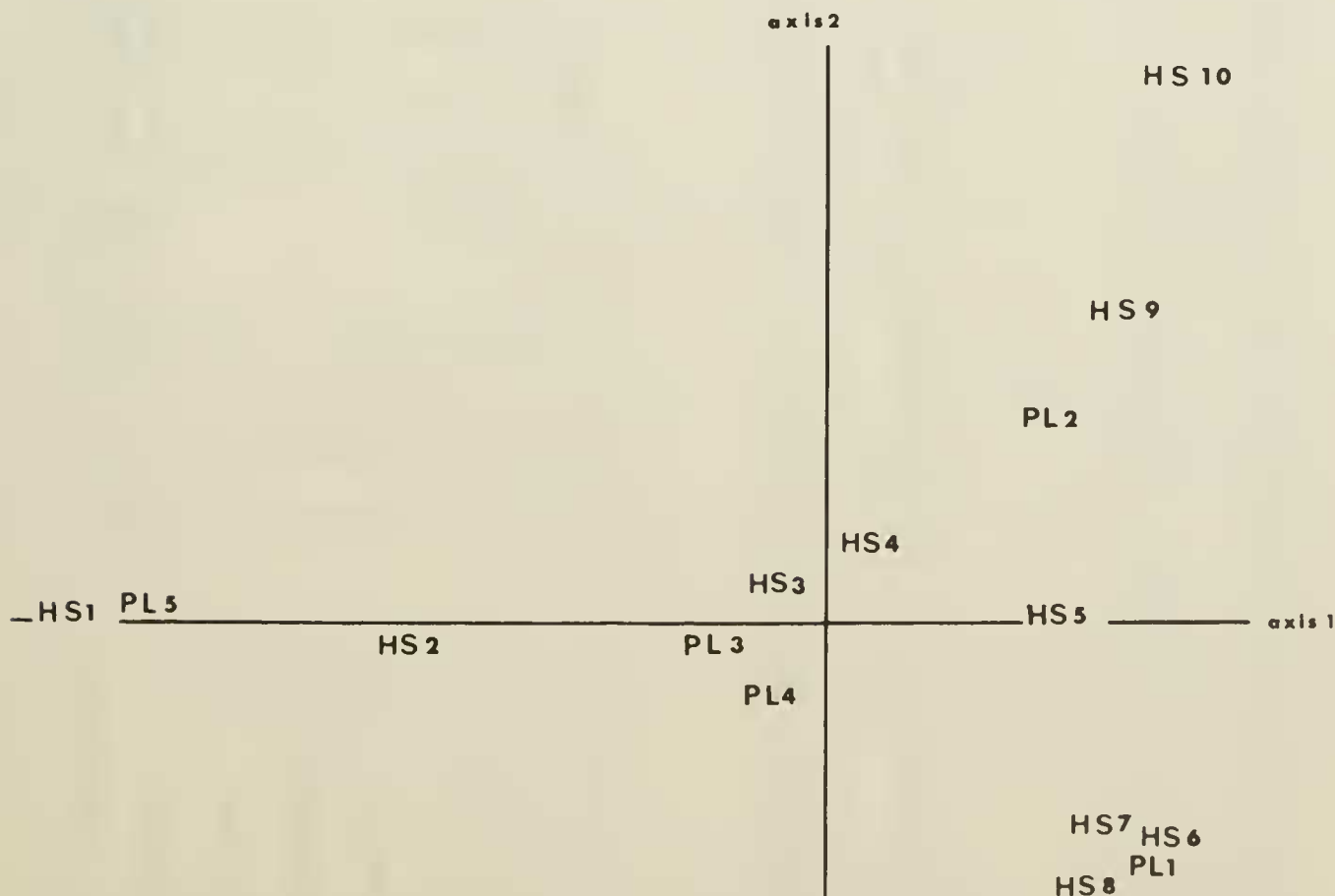


FIG. 12. Factor analysis of the contingency table of the variables rainfall (PL) and shape (HS). Projection of the variables. Axis 1: proper value 0.38, inertia 66%; axis 2: proper value 0.15, inertia 26%.

TABLE 3. Limit values for the modality PL used in Fig. 12 (in mm rainfall/year).

PL1	PL2	PL3	PL4	PL5
950, 1150	1150, 1500	1500, 2125	2125, 2750	2750, 3500

TABLE 4. Limit values for the modality HS (ratio H/D) used in Fig. 9.

HS1	HS2	HS3	HS4	HS5	HS6	HS7	HS8	HS9	HS10
1, 63; 1, 91	1, 91; 2, 05	2, 05; 2, 12	2, 12; 2, 17	2, 17; 2, 21	2, 21; 2, 26	2, 26; 2, 3	2, 3; 2, 4	2, 4; 2, 54	2, 54; 3, 03

TABLE 5. Limit values for each modality in Figs. 13-16. HS = H/D ratio; HD in square units of 20 μm each; PL = rainfall in mm/year.

	PL1	PL2	PL3	PL4	PL5	HD1	HD2	HD3	HD4	HD5	HS1	HS2	HS3	HS4	HS5
<i>mariei</i>	950	1000	1200	1900	2100	3078	3588	3928	4439	4949	1.804	2.071	2.14	2.204	2.293
	1000	1200	1900	2100	3500	3588	3928	4439	4949	6480	2.071	2.14	2.204	2.293	2.694
<i>boucheti</i>	1500	1900	2500	3000	3500	2590	3005	3254	3669	3669	1.73	1.831	1.895	1.939	1.983
	1900	2500	3000	3500	3500	3005	3254	3669	4250	4250	1.831	1.895	1.939	1.983	2.135
<i>nissidiophila</i>	1125	1190	1200			2240	2653	3066	3480	3893	1.93	2.1	2.184	2.336	2.54
	1190	1200	1250			2653	3066	3480	3893	4995	2.1	2.184	2.336	2.54	2.946
<i>opaoana</i>	950	1000	1658	1900	3000	5040	5700	6000	6580	7460	1.81	2.106	2.179	2.24	2.29
	1000	1658	1900	3000	3000	5700	6000	6580	7460	9440	2.106	2.179	2.24	2.29	2.549
<i>montrouzieri</i>		950	1200	2200	2300	5565	8407	9038	9670	10500	1.629	2.039	2.121	2.202	2.284
	1200	2200	2200	2300	3500	8407	9038	9670	10500	11880	2.039	2.121	2.202	2.284	2.448

The station numbers (used because they make an analysis much easier than coordinates) were introduced as supplementary columns, which means that they do not influence the analysis but are projected on the diagrams. The class limits for each modality in each species are given in Table 5.

The projection of the variables for *Palaina nissidiophila* is shown in Fig. 13. The cline for size from north (sta. 1) to south (sta. 14) is clearly shown, and appears to be linked to increase of rainfall. In the northern part of the range (stas. 1–6) stouter shells are found in higher rainfall, but in the southern part of the range (sta. 14) the shells become more slender whereas rainfall increases. This apparent aberration will be analysed further.

I can analyze the variations of *Palaina montrouzieri* only over the northern half of New Caledonia (it is known from the southern half only from the type-specimen). The projection in Fig. 14 shows a correlative variation of shell size and shell shape from stout small shells to large slender shells. Along axis 1, relatively small shells are associated with lower rainfall whereas the relatively large

shells are associated with relatively high rainfall. The very high rainfall PL5 is opposed to all the lower rainfalls along axis 2. The interpretation, with stations, is a very clear cline for size and shape from the Tiébaghi to Lindéralique (stas. 4, 9, 10, 11) related with the increase of rainfall. Inside this cline several clines for shape are induced by very high rainfall at stations 8, 17 and 20, which are all on mountains where rainfall is much higher than in surrounding lowland area. The Pompei specimens (sta. 13) have a stout shape linked to high rainfall, but are abnormally large; that is why station 13 is farther left on the diagram than the other equivalent stations. A tentative explanation will be given later.

Palaina mariei is, at first sight, a different case compared with the two preceding species. When examining the scatter of the different populations on a H/D diagram, variations look geographically random and no clines are obvious except over a very short distance, which raises doubt about interpretation. However, the projection of the variables on the (1, 2) plane as shown in Fig. 15 is

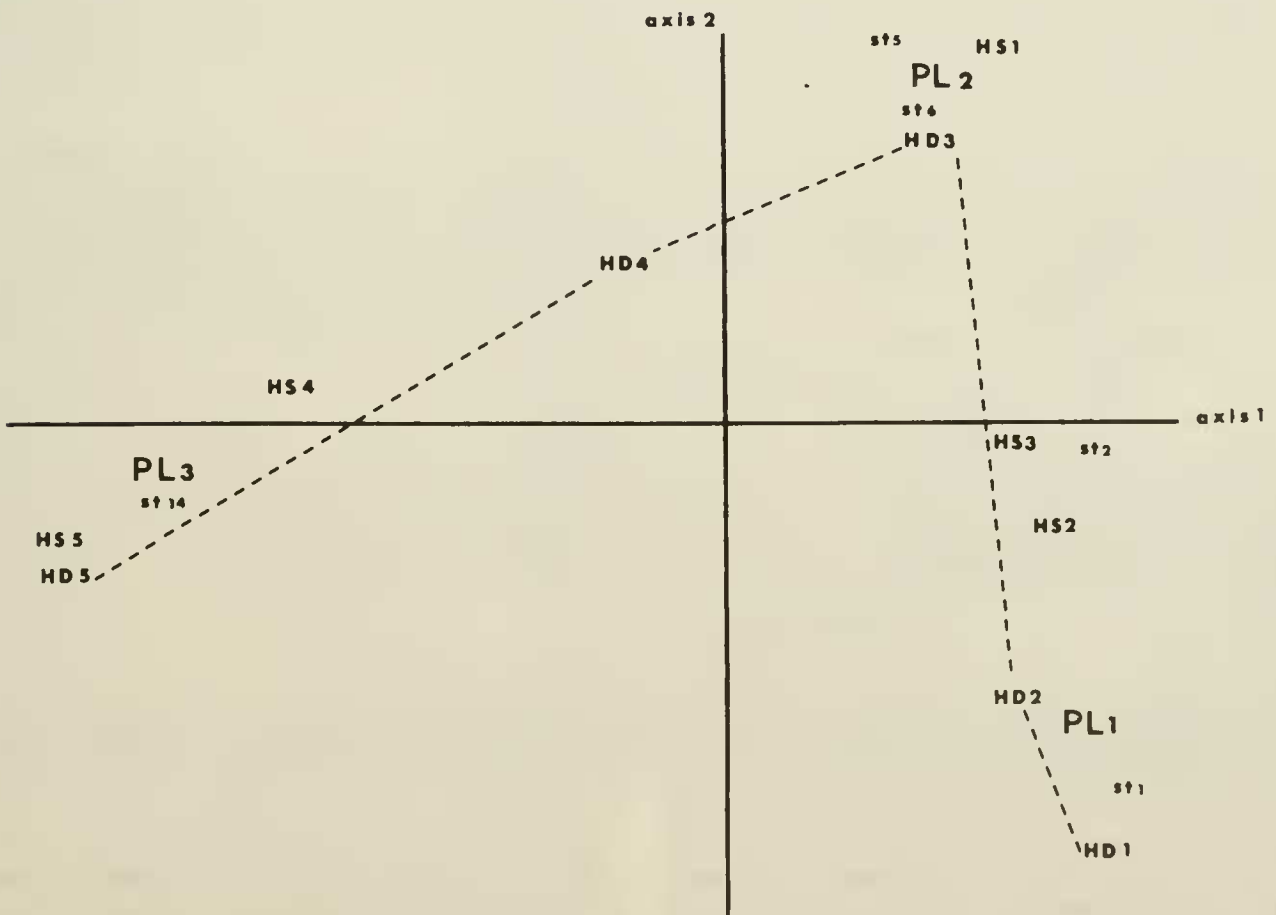


FIG. 13. Factor analysis of *P. nissidiophila* for rainfall (PL), size (HD) and shape (HS); projection of the variables and of the stations. Axes 1 and 2 have respectively 0.88 and 0.57 as proper values and represent 26% and 17% of the variance.

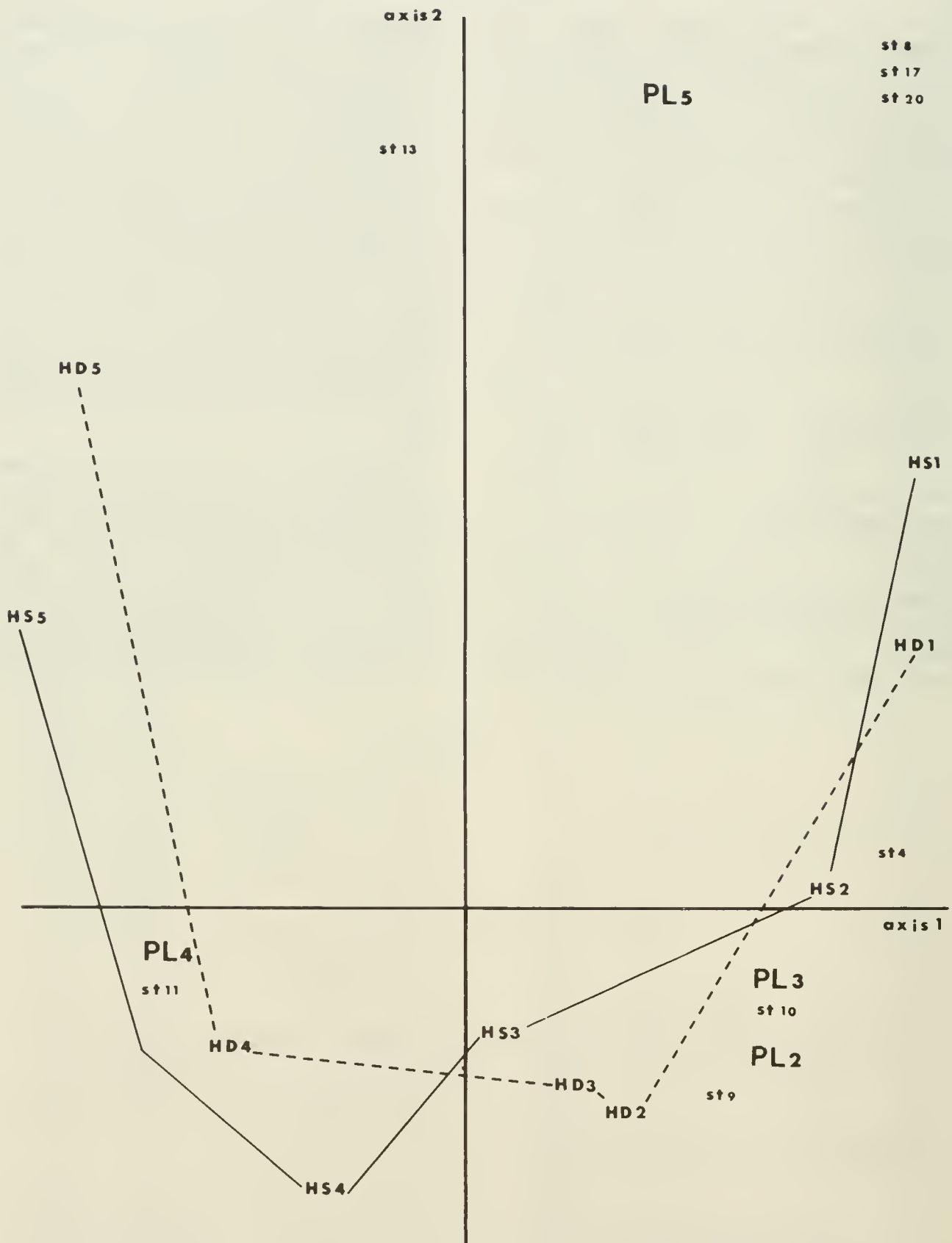


FIG. 14. Factor analysis of *P. montrouzieri* for rainfall (PL) size (HD) and shape (HS); projection of the variables and of the stations. The axes 1 and 2 have each 0.72 and 0.53 as proper values and represent 20 and 15% of the variance.

clear. Large and slender shells are associated with very low rainfall, small and stout shells with high rainfall and very stout shells with very high rainfall. As the species occupies a geographic range exhibiting a climatic patch-

work, the clines caused by the same mechanism as the preceding ones cannot be observed over a distance exceeding a few tenths of a kilometer and, as a result, geographic variations look random.

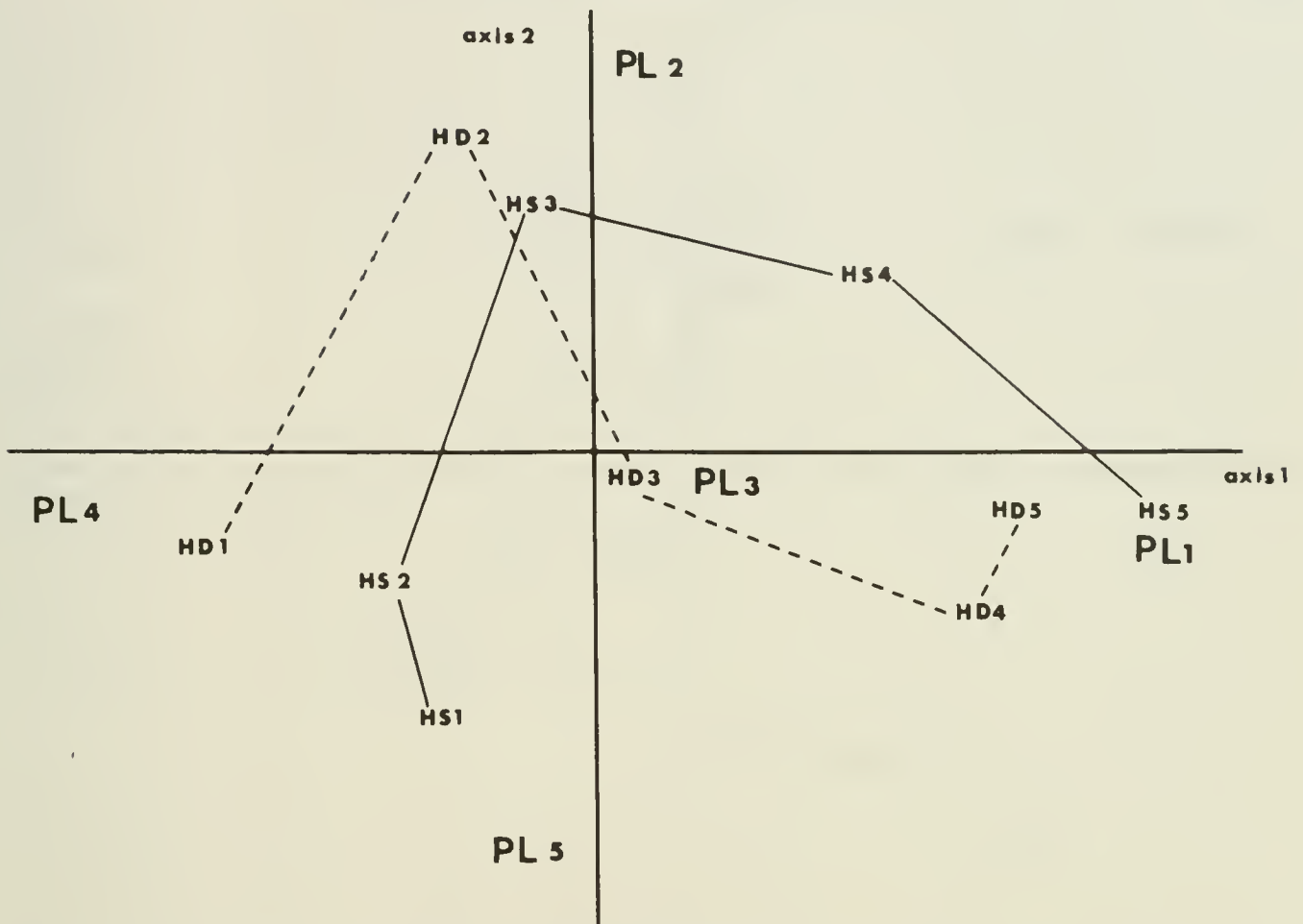


FIG. 15. Factor analysis of *P. mariei* for rainfall (PL), size (HD) and shape (HS); projection of the variables. The axes 1 and 2 have each 0.64 and 0.49 as proper values and represent 16% and 12% of the variance.

Palaina boucheti (Fig. 16) shows the same trends as *P. mariei*. A cline of increasing sizes from high to low rainfall is seen, together with a cline for shape associating the two stoutest classes with the two highest rainfalls and the three most slender classes with the two lowest rainfalls.

A similar diagram for *Palaina opaoana* is impossible to interpret, except for the association of large sizes and high rainfall. This may be due not only to large differences in sample sizes (50% of the specimens in a single station), but also to interaction with *Palaina montrouzieri*.

In conclusion it may be said that rainfall (and thus moisture) influences both size and shape. Its effect on shape is constant, but size increases with rainfall in some species and decreases in some others. Rainfall possibly does not directly influence shell size. This action of rainfall may explain the large clines in the northern mainland where climatic change is continuous over large distances, as the apparent random variation which is found further south and east; the latter being in fact clines

over small distances. However, influence of rainfall does not explain all the observed variation. The hypothesis involving species interaction will now be explored.

Interaction of species and character displacement

Peake (1973) remarked that sympatric species of Solomon Islands diplommatinids do not overlap morphologically. Fig. 8 shows that, in New Caledonia, there are large zones of overlap of the morphological scatter of the species when all populations are considered. However, there is not one case where there is morphological overlap where species were collected together. The data on allopatry and sympatry are summarized in Table 2. The species which converge when allopatric and diverge when sympatric are: 1) *Palaina nissidiophila* and *P. mariei* in station 14; 2) *P. mariei* and *P. boucheti* in stas. 20, 50, 51, 52; 3) *P. opaoana* and *P. mariei* in stas. 21, 22, 27, 28; 4) *P. montrouzieri* and *P. opaoana* were found only to be allopatric, but in the

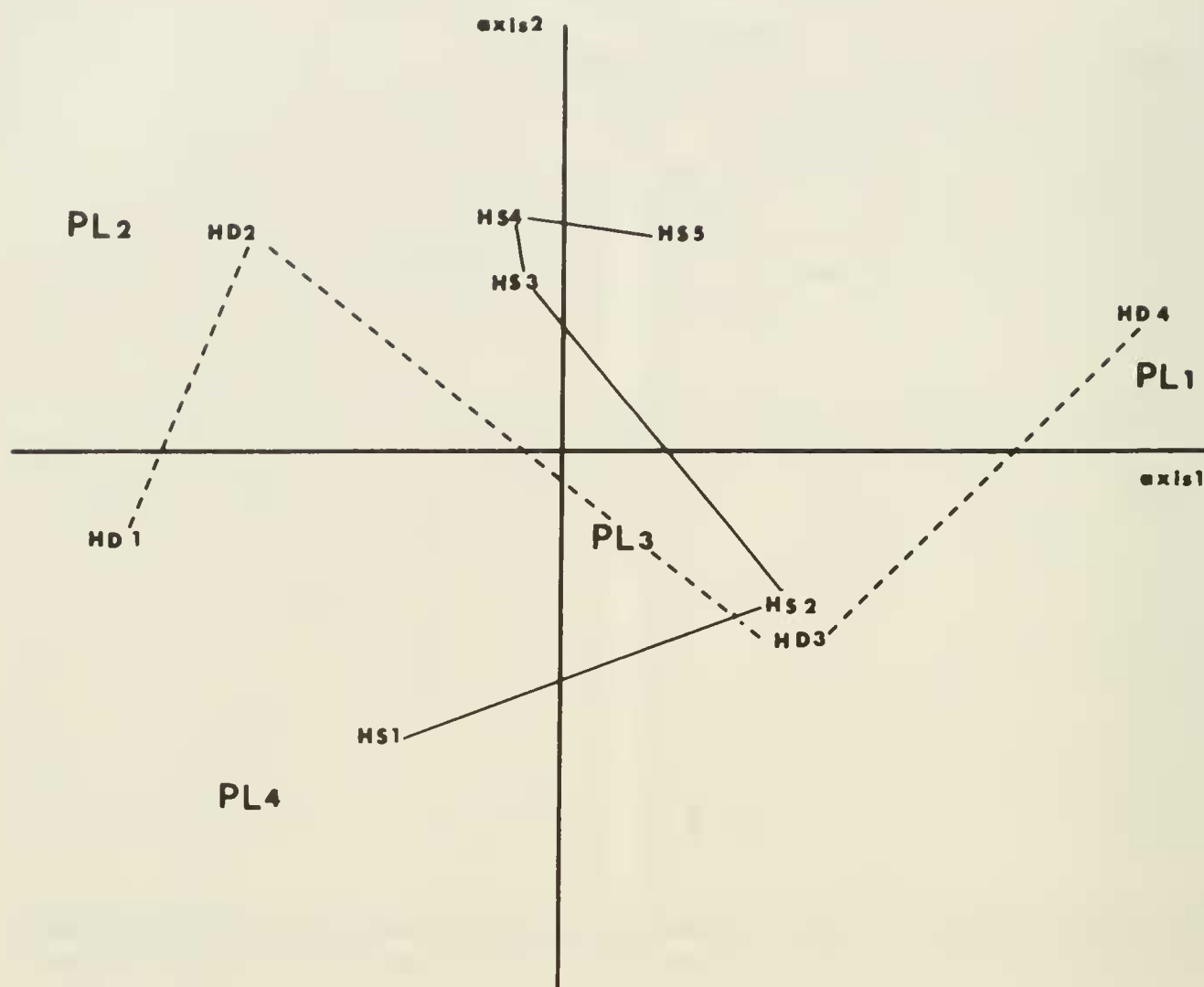


FIG. 16. Factor analysis of *P. boucheti* for rainfall (PL), size (HD) and shape (HS); projection of the variables. The axes 1 and 2 have respectively 0.62 and 0.45 as proper values and represent 19% and 14% of the variance.

same geographic range. *Palaina obesa* and *P. nanodes* were found sympatric with only much larger species.

In most cases it is the size scatter of the populations which appear reduced to avoid the overlap. An example is given for *Palaina opaoana* and *P. mariei* in Nindiah (sta. 22) as illustrated in Fig. 14. The displacement of size caused by sympatry may also be the origin of the aberrant position of station 13 (Pombeï) in Fig. 11. In the cline of *Palaina montrouzieri*, this station appears to be a good intermediate between dry and wet stations of the northeastern coast, but shell size is larger than expected there. This may be related with the fact that the largest *Palaina boucheti* were found in this station, fitting in their cline for size and rainfall.

In only one case do we have evidence for character displacement in shape. As seen in Fig. 10, *Palaina nissidiophila* has a clinal variation from northern small sizes to south-

ern larger sizes, correlated with a normal variation of the shell shape in the northern part of the range which abnormally reverses in the southern part. Between the region of Koumac (stas. 5, 6) and the Faténaoué valley (sta. 14), shells were expected to become stouter as rainfall increases but become more slender. In fact, as shown in Fig. 18, the place where the cline for shape reverses is the northern limit of the area of *Palaina mariei*, the scatter of which on a H/D diagram is the one which would have been expected for *P. nissidiophila* in this region.

Two solutions may be proposed here to explain these character displacements. If we admit that competition for food occurs, which is quite possible as far as all species have the same radula, differences in shell shape and/or size could allow sympatric species to exploit different sizes of interstices in the same leaf litter; or the presence of several species in the same leaf litter could cause

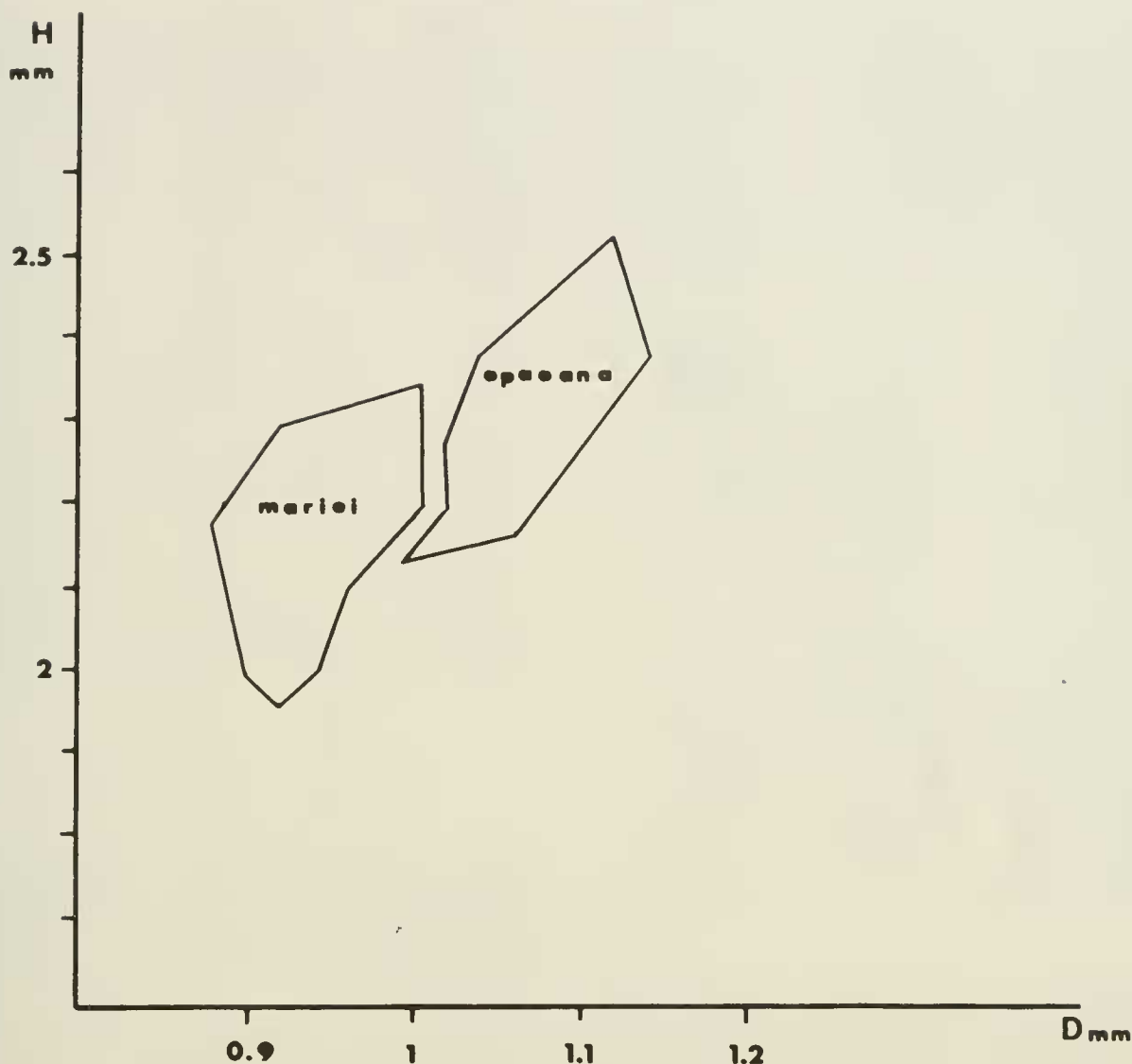


FIG. 17. Reduced scatter of H and D in sympatric *P. opaoana* and *P. mariei* from Nindiah (sta. 22). Compare with the scatter of the whole species, Fig. 8.

them to live outside of their optimal range of moisture, so that different shell shapes or sizes would be selected. On the other hand, males have no penis and if individuals do not recognize each other chemically for mating (which we do not know), we can postulate that they recognize each other by shell shape and size. Thus the animals having the same shape and size, but belonging to different species, would be less successful in reproduction, often mating with the wrong partners, and would be eliminated generation after generation, provoking the morphological divergence of sympatric populations. Of course the observed character displacements can also be the result of the combination of factors proposed here as well as some others that we do not suspect.

As character displacement seems so common, the observed clinal variations in New Caledonian diplommatinids could be the re-

sult of coevolution of species having adjacent scatters for H and D. The final and purely theoretical stage of such a coevolution, which can never be attained because environment is not constant through time, would be the establishment of parallel clines of all species over all of mainland New Caledonia. Several tests have been made to try to demonstrate the interdependency of the clines of the various species, this interdependency being interpretable as the result of such an evolutionary process. Unfortunately, and as only factor analysis could be accepted for methodological reasons explained earlier, the results were not more conclusive than the simple H/D diagrams. However two remarks can be made: First, the clines of *Palaina mariei* and *P. boucheti*, which both occur over nearly all the mainland, are roughly parallel (Figs. 15, 16), so that identical shells are found in both species, but in different environmental conditions:

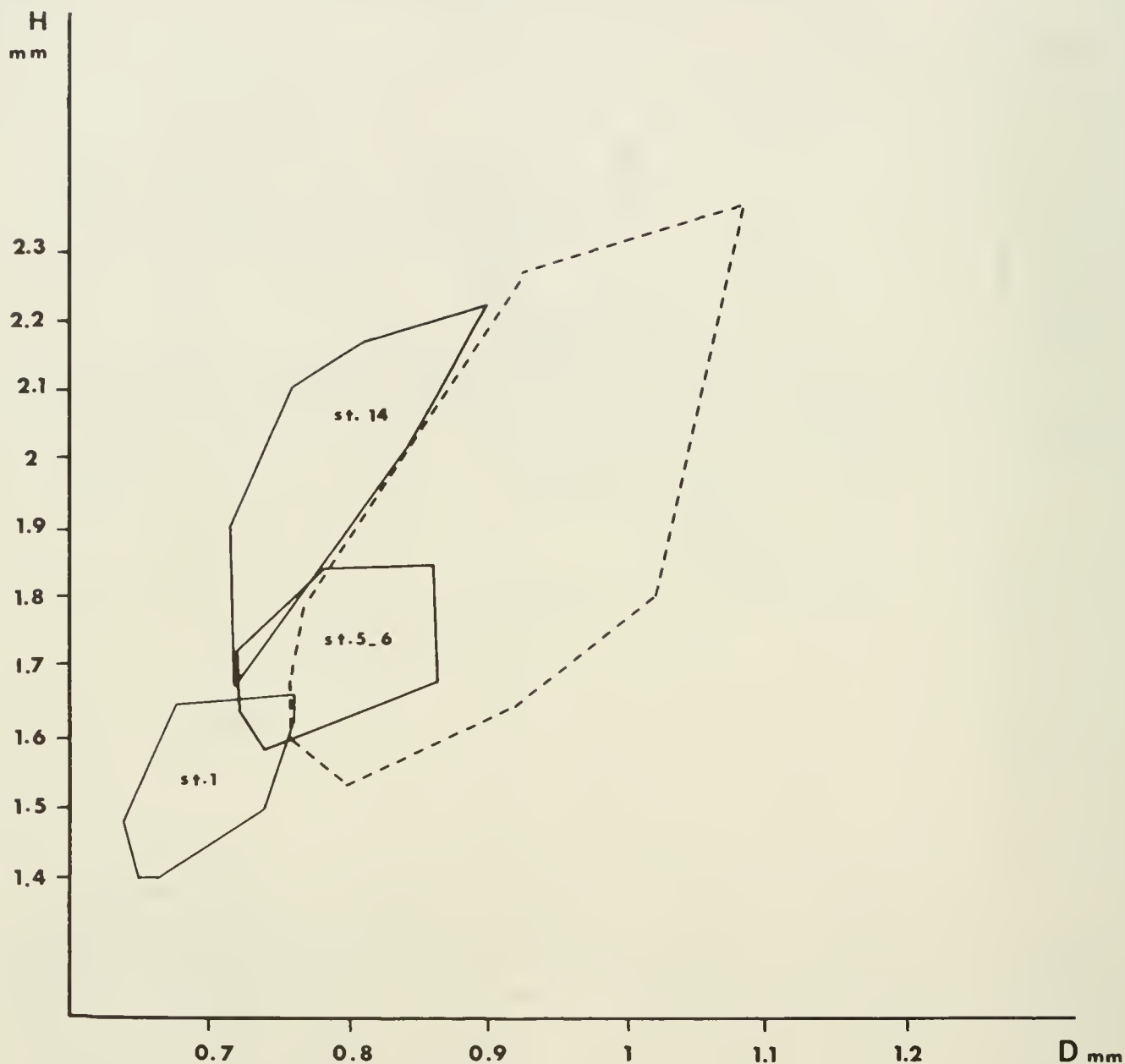


FIG. 18. Character displacement in shell shape of *P. nissidiophila*. Clinal scatter from sta. 1 to sta. 14 in full lines; scatter of *P. mariei*, sympatric with *P. nissidiophila* in sta. 14, in dotted line.

that is shown by the shells of the Figures 211 and 24B–24D, but the *P. mariei* shell comes from the extreme south whereas the *P. boucheti* shells come from the extreme north. Secondly, *Palaina montrouzieri* and *P. opaoana* seem to exclude each other over the entire geographic range of the latter. In central western New Caledonia, only *Palaina opaoana* was found at low altitudes and only *P. montrouzieri* was found at high altitudes. Shapes correlated with the rainfall found in this region are missing in the H/D diagram of *P. montrouzieri* (Fig. 8), and we have seen that no interpretable cline is found in the known material of *P. opaoana*. This could indicate species interaction on a large scale.

Implications for diplommatinine systematics

As the shells vary so enormously, no one considering only a few samples representative of the extreme forms would hesitate to consider them as belonging to different species. As nearly all diplommatinine species have been described from single samples, it is probable that a large proportion of the specific names are synonyms.

It has already been demonstrated that four states are found in female genital apparatus. These four states probably represent four steps of the same evolutionary process but, although I believe that this process is the loss of the seminal receptacle, I have no argument

which proves that it is not the acquisition of the receptacle. The steps of this process are found in all parts of Melanesia, and probably over the entire range of the Diplommatinidae. On the other hand, the species found in one region look more similar to each other than to the species found elsewhere. For example, nine Solomon Islands species have a mean H/D ratio of about 1.94, whereas New Caledonian species have a mean H/D ratio of about 2.16. Because we know that this ratio depends on rainfall in New Caledonia and because the Solomon Islands are wetter than New Caledonia, it is not possible to use this apparent general dissimilarity as a supraspecific character. Thus, in the *Diplommatina-Palaina* group, we have no argument, either anatomical or conchological, to determine what is convergence and what is monophyletism and as a result cannot at the moment discriminate any supraspecific group.

DESCRIPTION OF SPECIES

In the lists of materials, each sample is defined by the number of the station (locality indicated in Table 1 and Fig. 7) and the number of specimens in brackets. The abbreviations used are: AMS, Australian Museum, Sydney; MNHN, Muséum national d'Histoire naturelle, Paris; NMNZ, National Museum of New Zealand, Wellington.

Palaina montrouzieri (Crosse, 1874)

Figs. 19, 20

Diplommatina montrouzieri Crosse, 1874a: 110; Crosse, 1874b: 394, pl. 12, fig. 8 (Baie du Sud).

Palaina montrouzieri (Crosse), Franc, 1957: 41, pl. 4, fig. 48; Solem, 1961: 427; Kobelt, 1902: 401.

Diplommatina sp., Hedley, 1898: 103, fig. 11 (Oubatche).

Holotype: Baie du Sud, MNHN; Fig. 19B.

Other material: sta. 4 (12), sta. 8 (1), sta. 9 (> 50), sta. 10 (27), sta. 11 (> 50), sta. 13 (4), sta. 20 (4), sta. 17 (2).

Preserved material: sta. 4, sta. 10, sta. 11, sta. 13, sta. 20.

Geographic range: probably nearly all of New Caledonia, except the northern point and the western coastal border; possibly absent from the Mt. Guemba southeastern coastal

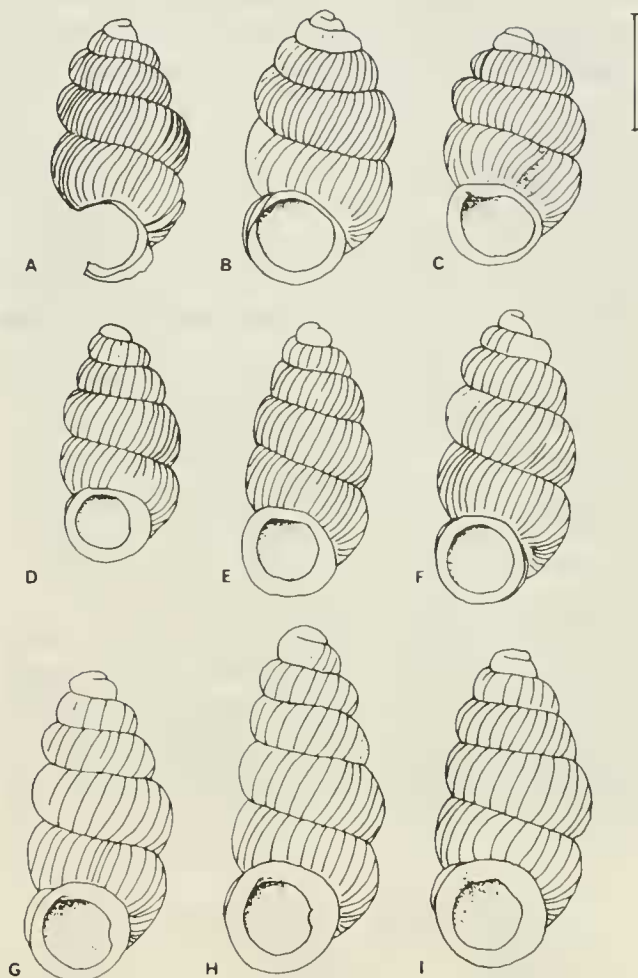


FIG. 19. Shells of *Palaina montrouzieri*. Scale line 1 mm. A, Aoupinié (sta. 17); B, holotype, Baie de Prony (sta. 51); C, Paéoua (sta. 20); D and E, Tiébaghi (sta. 4); F, Kaala (sta. 9); G and H, Lindéralique (sta. 11); I, Kavatche (sta. 10).

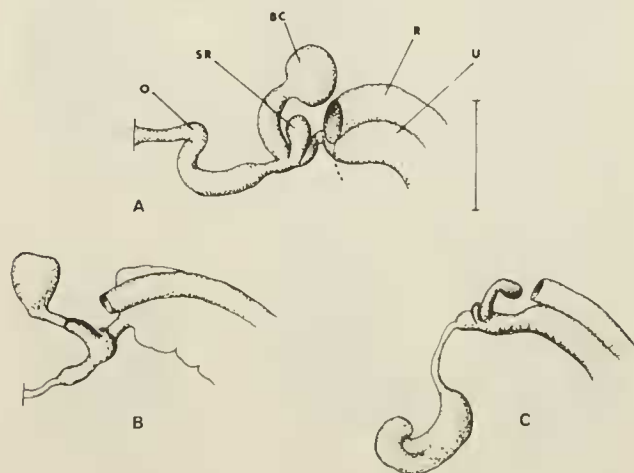


FIG. 20. Female genital anatomy of *P. montrouzieri*. Scale line 0.5 mm. A, Pombei (sta. 13); B, Lindéralique (sta. 11); C, Tiébaghi (sta. 4). BC, bursa copulatrix; O, oviduct; R, rectum; SR, seminal receptacle; U, uterus.

range. Although we did not collect it farther south than the Aoupinié (sta. 17), we have no reason to doubt the accuracy of the type locality.

Shell (Fig. 19): from 1.45×3.3 mm in Lindéralique (sta. 11) to 1.05×2.1 mm in the Tiébaghi (sta. 5) through a geographic cline. Stouter in the central range (Aoupinié), at high altitude in the western mountain masses (Paéoua) and in the southernmost region (Baie de Prony): from 1.4×2.4 mm to 1.24×2 mm. A small columellar tooth present in the northeastern coast samples, absent elsewhere. Radial ribs always *slightly oblique*, crowded at the middle, only slightly more crowded in the body whorl; more spaced in Lindéralique (sta. 11), closer when going farther from this locality in any direction.

Female genitalia (Fig. 20): bursa copulatrix rising upwards from the oviduct, with a nearly spherical head. Seminal receptacle a small elongated pouch, appressed along the bursa stalk but opening independently into the oviduct.

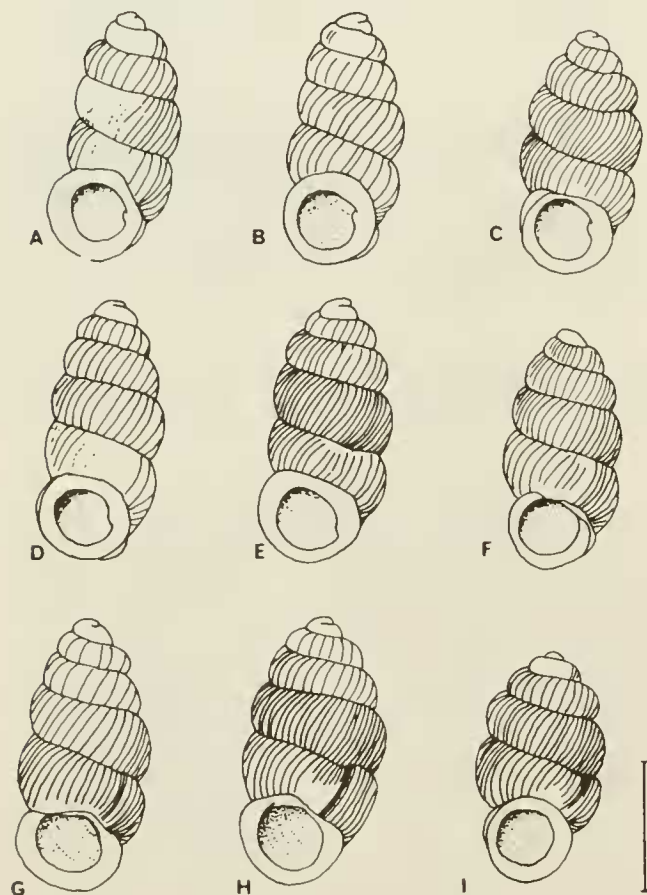


FIG. 21. Shells of *Palaina mariei*. Scale line 1 mm. A, Kaala (sta. 9); B, Nékliai (sta. 21); C, Poindimié (sta. 15); D, Plaine aux Gaiacs (sta. 23); E, Goipin (sta. 18); F, Mamié (sta. 44); G, lectotype, Nouméa (sta. 41); H, Baie de Prony (sta. 51); I, Mt. Oungoné (sta. 52).

Recognition: the only New Caledonian species with the seminal receptacle opening into the oviduct. Shell dimensions overlapping with those of *Palaina mareana*, *P. kuniorum*, *P. opaoana* and probably *P. mariei*. The latter is only smaller, and without anatomical data the distinction between the largest *P. mariei* and the smallest *P. montrouzieri* is delicate in the regions where they are potentially sympatric (see the case of the Nindiah population here attributed to *P. mariei*). *P. mareana* and *P. kuniorum* are always allopatric with *P. montrouzieri*; the former is more regularly conical, with more impressed sutures, more convex whorls and radial ribs much more spaced. *P. kuniorum* has the body whorl more constricted and has also radial ribs more spaced, particularly on the upper whorls, although less than in *P. mareana*. *P. opaoana* is potentially sympatric with *P. montrouzieri* and have about the same size. Apart from the anatomical differences, it is in most cases easily recognized by its radial ribs largely spaced on the first whorls and crowded on the last ones.

Remark: Franc's (1957) drawing of the holotype, "voluntarily" (*sic*) drawn without a camera lucida, is very different from the specimen, here depicted in Fig. 19B.

Palaina mariei (Crosse, 1867)

Figs. 21, 22

Diplommatina mariei Crosse, 1867: 179, pl. 7, fig. 6 (Nouméa).

Palaina (*Cylindropalaina*) *mariei* (Crosse), Kobelt, 1902: 408; Franc, 1957: 41, pl. 4, fig. 49; Solem, 1961: 428.

Palaina montrouzieri var. *humilior* Cockerell, 1930: 20, fig. 2; Solem, 1960a: 5; Solem, 1961: 428 (near Bourail).

Lectotype (here designated): Nouméa (sta. 41), MNHN; fig. 21G.

Paralectotypes: 2 specimens labelled "var. type" by Crosse + 1 shell from H. Fischer ex Crosse ex Marie, 1966—all in MNHN.

Other material: sta. 9 (50), sta. 10 (12), sta. 14 (5), sta. 15 (3), sta. 18 (2), sta. 19 (2), sta. 20 (2), sta. 21 (36), sta. 22 (39), sta. 23 (>50), sta. 24 (3), sta. 28 (40), sta. 26 (1), sta. 27 (2), sta. 31 (6), sta. 32 (1), sta. 33 (6), sta. 38 (1), sta. 39 (numerous juv.), sta. 40 (2), sta. 42 (2), sta. 44 (2), sta. 49 (3), sta. 50 (1), sta. 51 (13).

Preserved material: sta. 9, sta. 15, sta. 18, sta. 19, sta. 21, sta. 24, sta. 27, sta. 28, sta. 31, sta. 39, sta. 42, sta. 44, sta. 49.

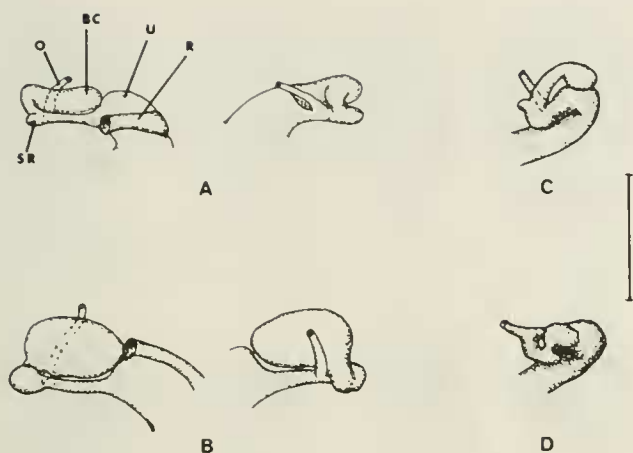


FIG. 22. Female genital anatomy of *P. mariei*. Scale line 0.5 mm. A and B, Mé Maoya (sta. 28); C, Baie Tina (sta. 42); D, Col des Roussettes (sta. 26). BC, bursa copulatrix; O, oviduct; R, rectum; SR, seminal receptacle; U, uterus.

Geographic range: nearly all the mainland, except possibly the northern point and the northeastern mountain range. Frequent along the coastlines, rather uncommon in the central and southern ranges.

Shell (Fig. 21): dimensions varying from 1.1×2.4 mm to 0.8×1.6 mm probably through numerous clines. Stouter in the southernmost mainland, with dimensions reaching 1×1.8 mm to 0.86×1.7 mm on the Mt. Oungoné (sta. 52). A columellar tooth generally present farther north than Bourail, absent farther south. Radial ribs as in *P. montrouzieri*; more spaced along the western coast, closer when going eastwards, or southwards from Nouméa.

Female genitalia (Fig. 22): the basal part of the stalk of the bursa copulatrix prolongs the distal oviduct from which the proximal oviduct diverges inwards and upwards. The upper part of the stalk, which is longer than the basal one, bends back along the distal oviduct in such a way as the more or less inflated bursa head is appressed against the proximal end of the uterus. The seminal receptacle is a swelling which prolongs the basal part of the bursa stalk outside of the bend of the latter. Two dispositions are found: farther north than the Col des Roussettes (sta. 27), the basal part of the bursa stalk is parallel to the spire; farther south, it is bent downwards.

Recognition: only *Palaina obesa* has a similar female genital anatomy in New Caledonia. It is found only in the northeastern range, is smaller and has more spaced radial ribs on the upper whorls. The dimensions of the shells of *P. mariei* overlap with those ob-

served in *P. opaoana*, *P. boucheti* and *P. nissidiophila*, but it was found sympatric with all three. The former is generally larger, never has a columellar tooth, and has more widely spaced ribs on the upper whorls. *P. boucheti* is generally smaller, more cylindrical and has closer radial ribs on the upper whorls. *P. nissidiophila* has a shape varying from cylindrical to conical, but its sutures are less impressed and its whorls less convex than those of *P. mariei*; it also has much closer radial ribs, and a more oblique aperture.

Remarks: the specimen labelled by Crosse "var. B" is here selected as the lectotype because the two shells labelled "var. type" are very badly preserved.

No preserved specimen was obtained from Nindiah (sta. 22), and this sample could have been attributed to *P. montrouzieri*. It is here identified as *P. mariei* because shell dimensions are closer to those of the *P. mariei* found in the same region. If it proves to belong to *P. montrouzieri*, the character displacement shown in Fig. 14 would be much greater than proposed here.

Palaina obesa (Hedley, 1898)

Fig. 23

Diplommatina obesa Hedley, 1898: 102, fig. 10 (Oubatche).

Palaina (Macropalaina) obesa (Hedley), Kobelt, 1902: 410; Franc, 1957: 41–42, pl. 4, fig. 50.

Palaina obesa (Hedley), Solem, 1961: 428.

Type material (not seen): Oubatche, AMS (sta. 8).

Other material (preserved): sta. 7 (3).

Geographic range: northeastern range (= Chaîne du Panié).

Shell (Fig. 23A, C): from 1.4×0.75 mm to 1.6×0.8 mm, very stout. Columellar tooth present or absent. Radial ribs distinctly more widely spaced on the upper whorls than on the following ones.

Female genitalia (Fig. 23B): bursa stalk straight and rather short, perpendicular from the oviduct upwards. The seminal receptacle is a very short pouch, prolonging the distal oviduct through the basis of the bursa copulatrix. It opens into the stalk, and not directly into the oviduct.

Recognition: *Palaina obesa* is distinct from both *P. mariei* and *P. boucheti* by its female genital anatomy. A similar disposition is found in *P. mariei* but the portion of the bursa stalk between the oviduct and the semina-

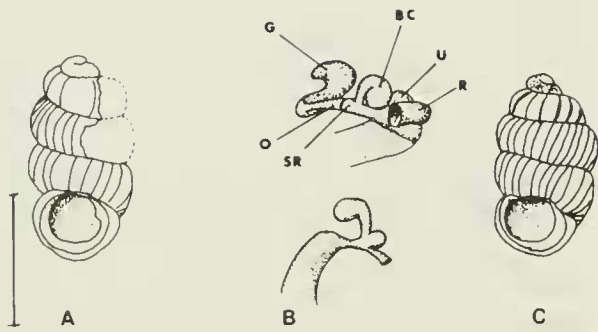


FIG. 23. *Palaina obesa*, Mandjéla, sta. 7. Scale line 1 mm. A and C, shells; B, female genital anatomy. BC, bursa copulatrix; G, gonad; O, oviduct; R, rectum; SR, seminal receptacle; U, uterus.

cle is much shorter in *P. obesa*. The shell differs from the shell of *P. mariei* by its smaller size and by the more widely spaced radial ribs of the upper whorls. *P. obesa* is convergent with the smallest *P. boucheti*, except for the anatomy and the spacing of the ribs; but the latter reaches its maximum size in the north-eastern region where it is potentially sympatric with the much smaller *P. obesa*.

Palaina boucheti Tillier, n.sp.

Figs. 24, 25

Holotype: Mé Ori, 530 m, P. Bouchet coll. 30.4.1979 (sta. 29), MNHN.

Paratypes: 11, same locality.

Other material: sta. 12 (14), sta. 13 (10), sta. 16 (1), sta. 20 (4), sta. 36 (1), sta. 45 (1), sta. 46 (3), sta. 47 (8), sta. 48 (12), sta. 50 (34), sta. 52 (4), sta. 51 (4).

Preserved material: type locality, sta. 12, sta. 13, sta. 20, sta. 46, sta. 47, sta. 48.

Geographic range: central New Caledonia farther south than Kaala-Gomen; absent from the western coastal plains and probably from the eastern coastline; probably replaced by *P. obesa* to the northeast of its range. Littoral only around the southernmost range, from the Ouinné river to the Baie de Prony.

Shell (Fig. 24): from 0.86×1.7 mm to 0.75×1.4 mm in the type series, reaching 1×1.7 mm to 0.86×1.8 mm elsewhere. Generally smaller and more cylindrical than *P. mariei*. A columellar tooth present or absent in northern New Caledonia (Taom sta. 12, Pombei sta. 13, Paéoua sta. 20), always absent farther south.

Female genitalia (Fig. 25): no seminal receptacle. The bursa stalk goes downwards from the oviduct. Two dispositions are found: in western samples (sta. 20, sta. 12, sta. 29),

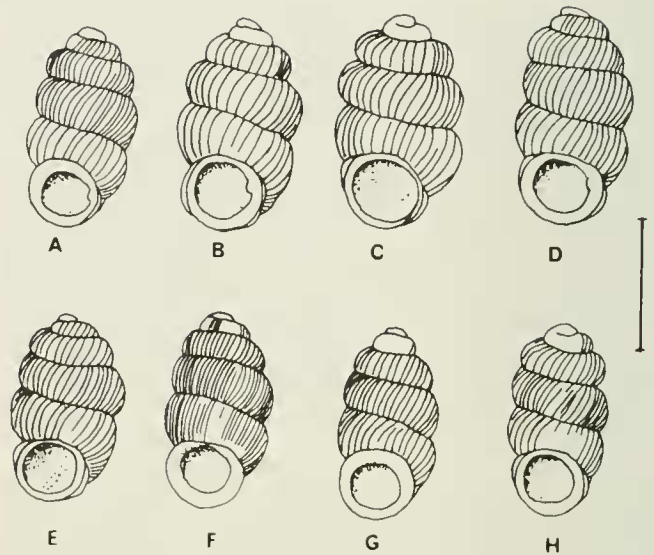


FIG. 24. Shells of *Palaina boucheti*. Scale line 1 mm. A, Taom (sta. 12); B and C, Paéoua (sta. 20); D, Pombei (sta. 13); E, Mt. Guemba (sta. 47); F, Touaourou (sta. 48); G and H, Mé Ori (sta. 29, paratypes).

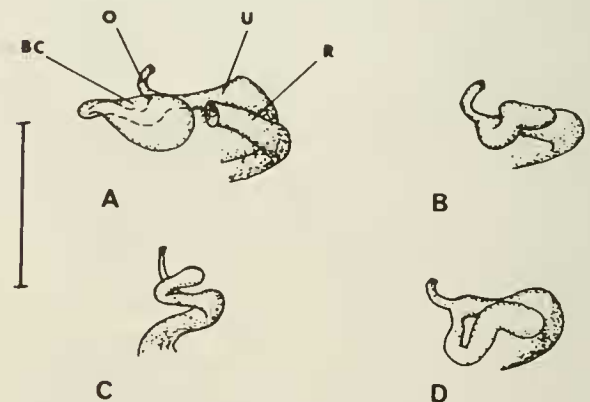


FIG. 25. Female genital anatomy of *P. boucheti*. Scale line 0.5 mm. A, Paéoua (sta. 20); B, Touaourou (sta. 48); C, Taom (sta. 12); D, Pombei (sta. 13). BC, bursa copulatrix; O, oviduct; R, rectum; U, uterus.

the basal part of the stalk runs parallel to the spire before bending upwards back to the proximal uterus, whereas in the eastern samples (sta. 13 to Touaourou sta. 48), the basal part of the stalk goes downwards parallel to the shell axis before bending back.

Discussion: the largest *Palaina boucheti* have shells completely convergent with the smallest *P. mariei* (Figs. 21I, 24D) but in different environmental conditions and in different parts of the common range of the two species. In such cases, dissection is necessary to check the presence or absence of a seminal receptacle. The dimensions of *P. boucheti* also overlap with those of *P. nissidiophila* which was never found sympatric with it, be-

ing a species found in dry environments in northwestern New Caledonia. *P. boucheti* has much more impressed sutures and rounded whorls, and much less crowded radial ribs.

***Palaina nissidiophila* Tillier, n.sp.**

Fig. 26

Holotype: Niénane (Iles Daos du Nord), Bouchet and Chérel coll., 23.8.78 (sta. 3), MNHN; Fig. 26B.

Paratypes (all dry): 9, same locality.

Other material (all dry): sta. 1 (50), sta. 2 (1), sta. 5 (21), sta. 6 (25), sta. 14 (50).

Geographic range: from Pott (Belep Islands) to the Koniambo mountain through Art, the Daos du Nord Islands, the northern point (probably) and the northwestern coastal plains.

Shell (Fig. 26): from 0.65×1.4 mm in Pott (sta. 1) to 0.85×1.8 mm in Koum (sta. 6) through a geographic cline, reaching 0.9×2.2 mm farther south. Suture not impressed and whorls generally only slightly convex; shape nearly cylindrical from Pott to Koum, becoming an elongated cone farther south. A small columellar tooth present in Le Cresson (sta. 5), present or absent in Koum (sta. 6), absent elsewhere. Peristome thicker than in other New Caledonian species, always oblique. Radial ribs always very crowded.

Discussion: the non-impressed sutures and the crowded ribs make *P. nissidiophila* easy to recognize. It is sympatric with *P. mariei* south of Koum (sta. 6) to the Koniambo (sta. 14) and thus there is no doubt about their specific distinction. Without anatomical data, there are less arguments for considering it as specifically distinct from *P. boucheti* which is always allopatric with it. The reason which makes me consider *P. nissidiophila* a distinct species is the large gap between it and *P. boucheti* in ornamentation and whorl contour. Geographically, they are found near one another.

***Palaina nanodes* Tillier, n.sp.**

Fig. 27

Holotype: Touaourou, 10 m, Bouchet coll. 8.12.1978 (sta. 48), MNHN.

Paratypes (8 preserved): 17 specimens, same sample.

Geographic range: *P. nanodes* was found only in Touaourou, but probably occurs along

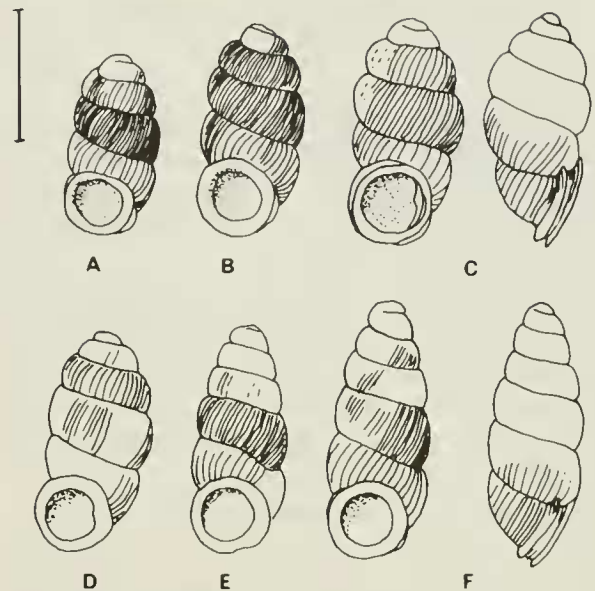


FIG. 26. Shells of *Palaina nissidiophila*. Scale line 1 mm. A, Pott (sta. 1); B, Holotype, Niénane (sta. 3); C, Le Cresson (sta. 5); D and E, Koum (sta. 6); F, Faténaoué (sta. 14).

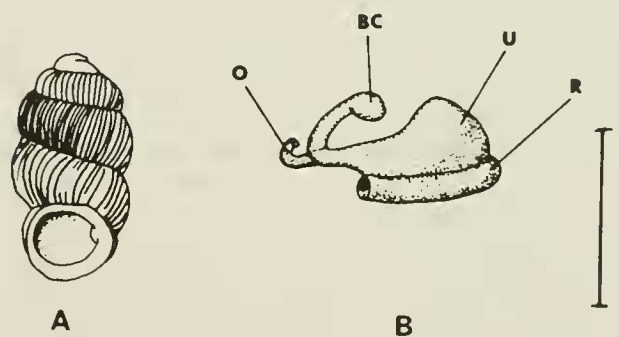


Fig. 27. *Palaina nanodes* Tillier, n. sp. Scale line A, 1 mm; B, 0.5 mm. A, shell; B, Female genital anatomy; both paratypes from Touaourou (sta. 48).

the coast, on the upraised reef between Yaté and Goro. At least one much bigger *Pararhytida* has the same odd range.

Shell (Fig. 27A): probably the smallest of all described *Palaina-Diplommatina* species, from 0.6×1.05 mm to 0.7×1.38 mm. Otherwise looks like a very small *P. boucheti*, but has closer radial ribs. Columellar tooth present or absent.

Female genitalia (Fig. 27B): no seminal receptacle. A very short portion of the bursa copulatrix stalk prolonging the distal oviduct, a much longer portion bent back upward to the proximal end of the uterus. A small rounded bursa head.

Discussion: there is no overlap for dimensions with any other New Caledonian species. The smallest *P. nissidiophila* are more slender (but found in drier conditions), with less impressed sutures, and *P. nanodes* was found sympatric with *P. boucheti*.

***Palaina kuniorum* Tillier, n.sp.**

Fig. 28

Holotype: Ouro, Ile des Pins, Bouchet coll. 21.10.1978. (sta. 53), MNHN; Fig. 28B.

Paratypes (all dry): 13, same sample.

Geographic range: Ile des Pins (called Kunié by Melanesians).

Shell (Fig. 28): in the only population collected, dimensions from 3.5×1.45 mm to 3×1.3 mm. Holotype 3.35×1.4 mm. No columellar tooth. Radial ribs rather widely spaced, closer on the body whorl. Body whorl distinctly constricted.

Discussion: the dimensions of *P. kuniorum* overlap those of *P. mareana*, which is easy to recognize by its more convex whorls and regularly conical shape. It seems closer to *P. montrouzieri*, from which it differs only by its more widely spaced radial ribs and more distinctly constricted body whorl. On the other hand the constriction of the body whorl is a variable character, but the form of *P. montrouzieri* from Lindéralique (sta. 11; Fig. 19G, H), which is the closest to *P. kuniorum* by its loose radial ribbing, has a more regularly conical shape (both are found on calcareous soils: does this allow a faster growth?). All the specimens of *P. montrouzieri* approaching *P. kuniorum* by their shell characters come from northern New Caledonia, but we know only the holotype as coming from the southern regions and may suspect that it is not very representative of the southern populations of *P. montrouzieri*. Lastly, there is a low probability for *P. montrouzieri* to occur along the coast of the mainland between Yaté and the Baie de Prony, that is the closest to the Ile des Pins and where P. Bouchet already collected four species. All these arguments

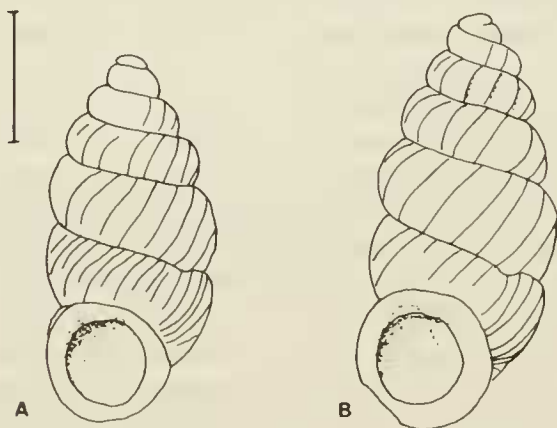


FIG. 28. *Palaina kuniorum* n. sp. Scale line 1 mm. Ouro, Isle of Pines (sta. 53). A, paratype; B, Holotype.

are contradictory, and the status of *P. kuniorum*, species or subspecies, will remain dubious as long as its female genital anatomy is not known. I have considered it a species because it could as well be related to *P. opaoana*, *P. mareana*, *Palaina* sp. or even to *P. perroquini* as conchological characters prove to be so variable.

***Palaina perroquini* (Crosse, 1871)**

Fig. 29

Diplommatina perroquini Crosse, 1871: 204; 1873: 44, pl. 12, fig. 8 (New Caledonia).

Palaina (Macropalaina) perroquini (Crosse), Kobelt, 1902: 410; Franc, 1957: 42, pl. 4, fig. 51.

Palaina perroquini (Crosse), Solem, 1961: 428.

Type material: the specimen depicted by Franc as the holotype, here redrawn in Fig. 29A, is probably not even type material: judging from the label it was given by Marie to Crosse in 1873, and we do not know whether

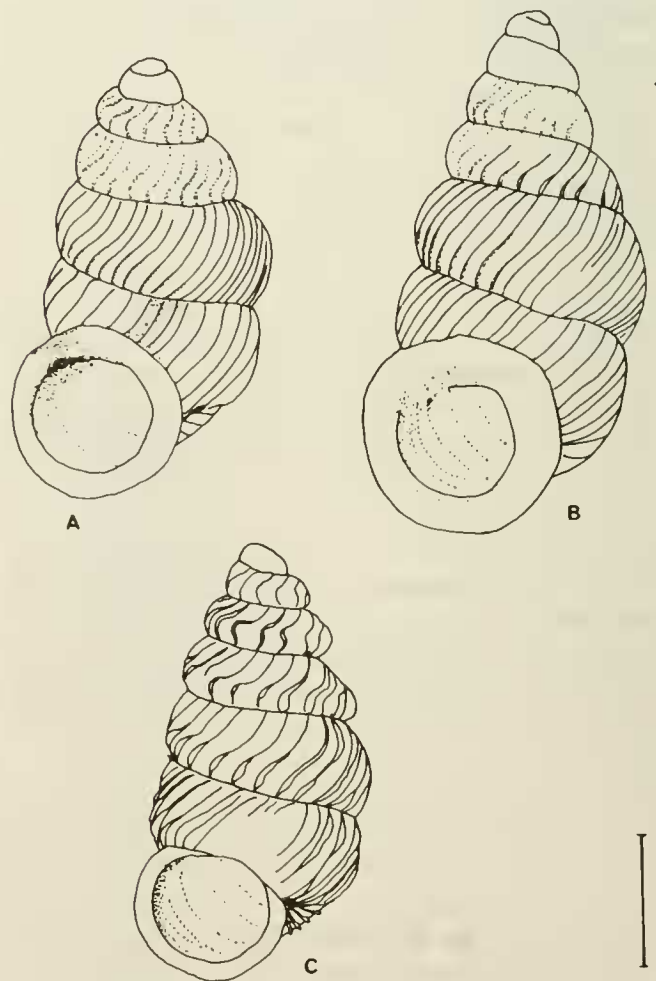


FIG. 29. *Palaina perroquini*. Scale line 1 mm. A and B, Baie de Prony (sta. 51) (A = specimen depicted as the holotype by Franc); C, Mt. Guemba (sta. 47).

Crosse had seen it previous to his first description in 1871. Two other samples, containing fifteen shells, are housed in the MNHN as acquired by Crosse from Petit in 1874. They are possibly syntypes, collected by Perroquin and given to Petit before 1871, and then acquired by Crosse, but we have no evidence to confirm that Crosse had seen them before his first description of the species. If necessary, Franc's "holotype" should be selected as a neotype, but *P. perroquini* is so easy to recognize that a neotype is not needed.

Other material: sta. 43 (1 + juv.), sta. 47 (4 + juv.), sta. 48 (3 + juv.), sta. 51 (14), plus about ten shells without accurate locality.

Preserved material: sta. 43, sta. 47, sta. 48.

Geographic range: southeasternmost part of the mainland, from the Yaté river to the Baie de Prony through the Plaine des Lacs, and further east to the coastline.

Shell (Fig. 29): from 1.5×3 mm to 1.85×4 mm. Regularly conical when tall, with penultimate whorl slightly inflated when short. Body whorl slightly constricted. No columellar tooth. Radial ribs *sigmoid on the upper whorls*, forming wing-like expansions in juveniles but more or less eroded in adults; more crowded on the last and often on the penultimate whorl.

Female genitalia: full adult not seen. In sub-adult females, the developing bursa copulatrix seems to be similar to the bursa found in *P. mareana* (Fig. 32), but I cannot be sure that there is no seminal receptacle at all outside of the bend of the bursa stalk, as is found in some Solomon Islands species and in the Australian *Palaina strangei* (Tillier, unpublished).

Recognition: the size, shape and sigmoid radial ribs of *P. perroquini* are not found in any other New Caledonian diplommatinid.

Palaina opaoana Tillier, n.sp.

Figs. 30, 31, 32

Holotype: junction of the rivers running down the Mé Maoya and the Pic Poya, alt. 50 m, Tillier and Bouchet coll. 15.6.1979 (sta. 28), MNHN.

Paratypes (preserved): 10, same sample.

Other material: sta. 21 (2), sta. 22 (39), sta. 27 (4), sta. 30 (5), sta. 34 (>200), sta. 35 (5), sta. 37 (3).

Preserved material: sta. 21, sta. 27, sta. 28 (type locality), sta. 30, sta. 35, sta. 37.

Geographic range: central western New Caledonia between the latitude of Houaïlou and the Dzumac range (the latter is the last

mountain before the southern lowland). Probably never littoral.

Shell (Figs. 30, 31): from 1.3×2.9 mm to 1.1×2 mm; may be stouter, reaching 1.25×2 mm on the Dzumac (alt. 1000 m; sta. 37), or much more slender, reaching 1.1×2.6 mm in the dry Col des Arabes (Figs. 31D, E; sta. 34). Close to *P. montrouzieri* by its size and shape, but the upper whorls more convex. Radial ribs widely spaced and *parallel to the shell axis on the upper whorls* (closer and oblique in *P. montrouzieri*), close and slightly oblique on the following ones.

Female genitalia (Fig. 32): no seminal receptacle. Bursa stalk going outwards and downwards from the oviduct before bending back parallel to the oviduct in the westernmost samples (sta. 37, sta. 28, sta. 21). In central and eastern samples, the bursa stalk goes downwards almost perpendicular from the oviduct and bursa head is in the centre of the intestinal loop instead of being appressed against the proximal end of the uterus. The intermediate position is found in the Col des Roussettes (sta. 27).

Recognition: differs from *P. montrouzieri* and from the largest *P. mariei*, which may

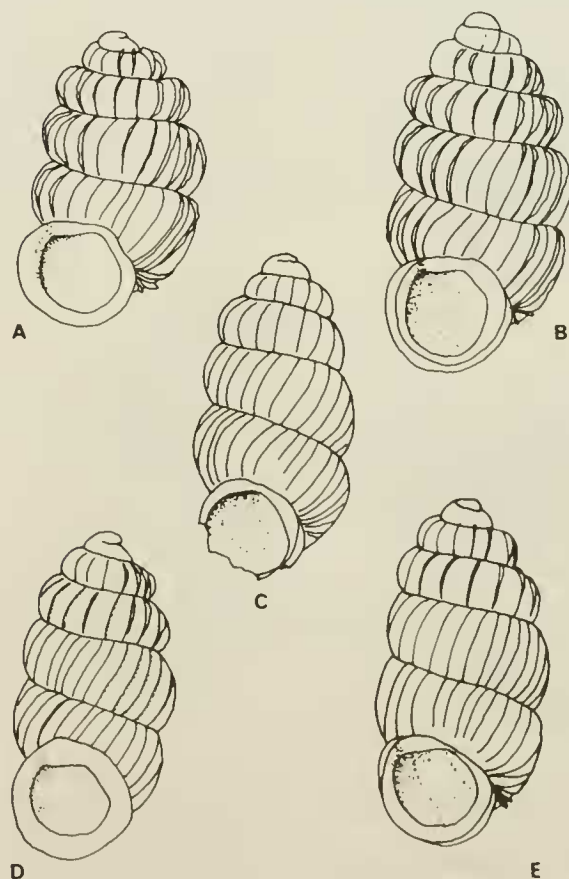


FIG. 30. Shells of *Palaina opaoana* Tillier, n. sp. Scale line 1 mm. A and B, Mt. Dzumac (sta. 37); C, Col des Roussettes (sta. 27); D and E, Mé Maoya (sta. 28); D, paratype; E, Holotype.

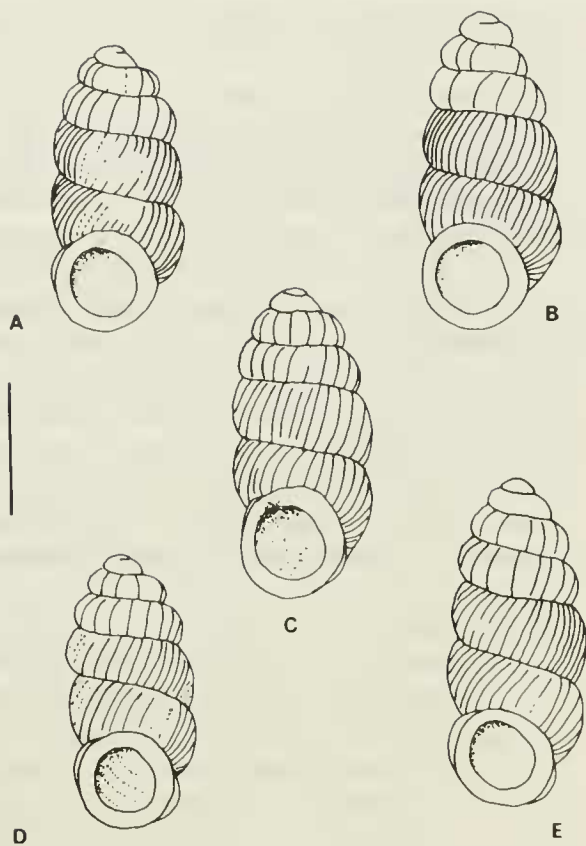


FIG. 31. *P. opaoana*. Scale line 1 mm. A and B, Dothio (sta. 30); C, Nassirah (sta. 35); D and E, Col des Arabes (sta. 34).

converge with it by their dimensions, by the female genitalia and by the radial ribs of the upper whorls. By shell size and genal anatomy, two geographic sets of population can be distinguished: one western, with larger shells (Fig. 30), and with the disposition of the bursa copulatrix shown in Fig. 32A, C; the second eastern, with smaller shells (Fig. 31) and the genital disposition shown in Fig. 32B; the transition is probably found nearby (intermediate found in the Col des Roussettes, sta. 27).

Palaina opaoana resembles the four (?) New Hebridean species, which have the same type of shell shape and sculpture, but whose anatomy is unknown.

***Palaina mareana* Tillier, n.sp.**

Figs. 33, 34

Holotype: Enéné, Maré Island, Bouchet coll. 7.4.1979 (sta. 54), MNHN.

Paratypes (preserved): 6, same sample.

Other material: sta. 55 (1), sta. 56 (5).

Preserved material: sta. 54 (type locality), sta. 56.

Geographic range: Maré Island, Loyalty Islands.

Shell (Fig. 33): from 1.4×3.7 mm to 1.2×2.8 mm, the largest shells being more regu-

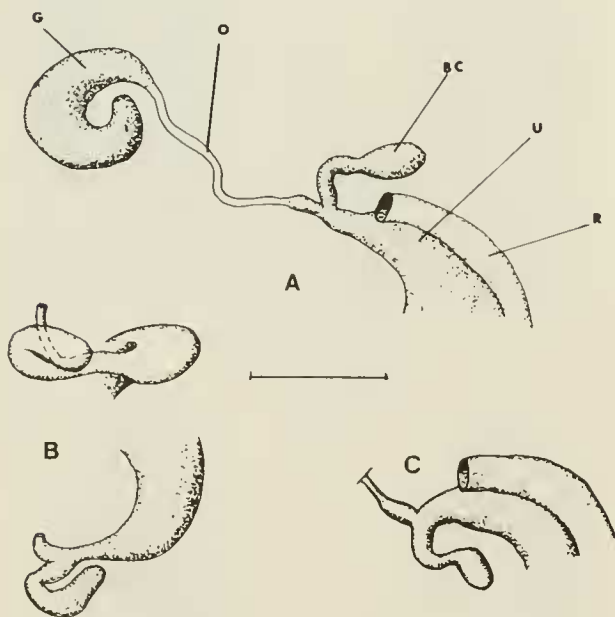


FIG. 32. Female genital anatomy of *P. opaoana*. Scale line 0.5 mm. A, Mé Maoya (sta. 21); B, Nassirah (sta. 35); C, Mt. Dzumac (sta. 37); BC, bursa copulatrix; G, Gonad; O, oviduct; R, rectum; U, uterus.

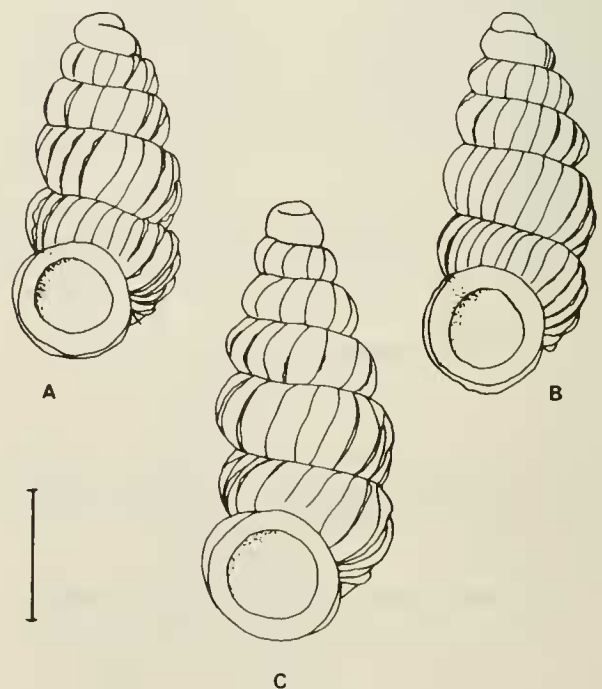


FIG. 33. *Palaina mareana* Tillier, n. sp. Scale line 1 mm. A and B, Nécé (sta. 56); C, Enéné (sta. 54), paratype.

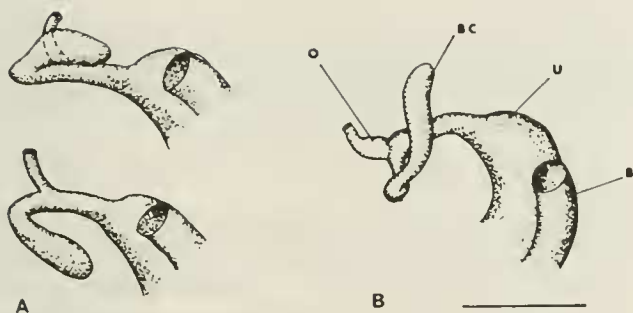


FIG. 34. Female genital anatomy of *P. mareana*. Scale line 0.5 mm. Paratypes, Enéné (sta. 54); BC, bursa copulatrix; O, oviduct; R, rectum; U, uterus.

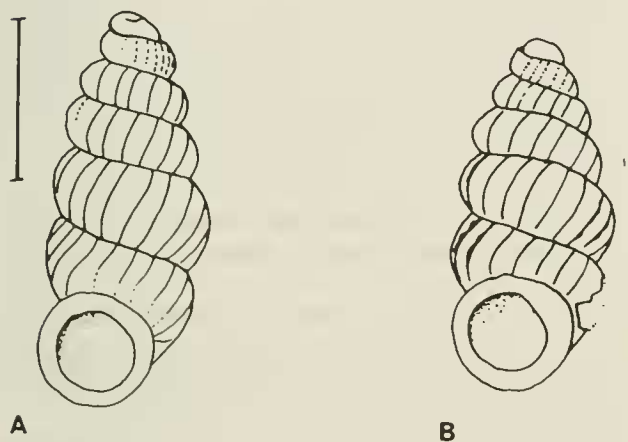


FIG. 35. Shells of *Palaina* sp., Adio (sta. 25). Scale line 1 mm.

larly conical than the smallest ones. Sutures impressed, whorls convex. Radial ribs always lamellar, widely spaced, often becoming slightly more crowded on the body whorl.

Female genitalia (Fig. 34): no seminal receptacle. Bursa copulatrix long and slender. Bursa stalk first running parallel to and under the oviduct and then bent back forwards to the proximal end of the uterus.

Discussion: distinct from any other New Caledonian species, the smaller *Palaina* sp. excepted, by its conical elongated shape, convex whorls and loose radial sculpture. Close to the Australian *P. strangei* in its shell characters, but the latter has a stouter shell and a seminal receptacle outside of the bend of the bursa stalk (Tillier, unpublished).

Palaina sp.

Fig. 35

Material (dry): three shells, the best preserved broken, sta. 25.

Geographic range: seems restricted to the calcareous outcrop of Adio (sta. 25).

Shell (Fig. 35): similar to *P. mareana* but smaller, the two preserved shells measuring 2.6×1.2 mm and 2.9×1.1 mm.

Discussion: although I do not believe it, these shells could be elongated *Palaina mariei* with a loose radial sculpture possibly due to the occurrence of calcareous rocks; but *P. mariei* is found unmodified on such rocks in Nindiah (sta. 22) and on the south-eastern upraised coral reef (sta. 45, sta. 49). I prefer to consider it a species which spread when calcareous rocks were not eroded and which is now restricted to the outcrop in Adio. If the elongated conical shape, convex whorls and loose sculpture are not correlated with calcareous rocks, *Palaina* sp. could be related with the Australian *P. strangei* and with *P. mareana*.

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